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Running head: ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

ANTHROPOGENIC IMPACTS AND INFLUENCE ON AFRICAN PAINTED DOGS
(*LYCAON PICTUS*)

A Dissertation

Presented to the Faculty of

Antioch University New England

Keene, New Hampshire

In partial fulfillment for the degree of

DOCTOR OF PHILOSOPHY

by

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June 2020



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(*LYCAON PICTUS*)

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ABSTRACT

ANTHROPOGENIC IMPACTS AND INFLUENCE ON AFRICAN PAINTED DOGS

(*LYCAON PICTUS*)

Tammy L. Cloutier

Antioch University New England

Keene, New Hampshire

Anthropogenic activity has been documented to have negative impacts on wildlife that include altered behaviors, lower body mass, and decreased reproductive success. Although wildlife viewing provides support for conservation efforts, it is also one of many human recreational activities that pose a threat to wildlife. The painted dog (*Lycaon pictus*) is a popular species for viewing by tourists, and one of Africa's most endangered carnivores. Anthropogenic-based actions such as persecution, snaring, diseases transmitted via domestic dogs, and habitat fragmentation contribute to their decline, and human disturbance at den sites, primarily via tourism, is an emergent threat for this species. I explored the potential effects of direct and indirect human activity on painted dogs during their denning season using a mixed method approach for free-ranging and captive populations. This included: (a) identifying areas where humans visited painted dog dens using social media posts and content analysis, (b) developing and testing a noninvasive measurement tool (belly score) to assess the body condition of painted dogs via images, (c) comparing carnivore and herbivore activity on human-modified game trails and unmodified game trails using camera traps, and (d) comparing feeding regimens and morphometric measurements between two captive painted dog litters. Results from this study showed that (a) painted dog dens have been visited by humans in at least seven of the 14 countries where painted dogs are known to exist, with the majority of visits reported in South

ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

Africa, (b) belly score means differed significantly between two populations of painted dogs (Hwange National Park and Mana Pools National Park, Zimbabwe) while seasonal variations were similar for both populations; demonstrating how this tool may be used to assess body condition, foraging success, and fitness between and among individuals and populations, (c) carnivores were observed on human-modified trails more frequently than unmodified trails, and herbivores were observed on unmodified trails more frequently than modified trails, though neither relationship was significant. Time of day each group was observed on both types of trails did differ significantly: carnivores were observed more frequently in the evening/overnight hours, and although herbivores were observed at similar levels during morning and mid-day hours, carnivore observations decreased during mid-day hours. (d) Limb length and body length ratios differed significantly between the two captive litters, suggesting that how animals are fed may have an influence on growth in human-managed wildlife populations, with implications for those individuals targeted for release into the wild or free-ranging populations facing food stress. Results from each aspect of this study can be used to inform wildlife managers, policy makers, the tourism sector, conservation professionals, and zoological facilities to assist with the management of this species and minimize impacts of human recreation. Further research is highly recommended for all topics discussed. This dissertation is available in open access at

AURA, <http://aura.antioch.edu/> and OhioLINK ETD Center, <https://etd.ohiolink.edu/etd>.

Keywords: ecotourism, recreation ecology, human disturbance, Zimbabwe, reintroduction, husbandry, diet, growth, anthropogenic disturbance, painted wolf, Africa, carnivore, endangered species, *in-situ*, *ex-situ*, conservation biology, wildlife conservation

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I am heartbroken that my dad did not live to see me become a “doctor,” but am grateful for our shared love of wildlife and hope I have done him proud. Despite not being able to keep up with half of what I was doing as I ran around the world, I absolutely appreciate my mom’s unwavering support, which included babysitting her furry granddaughter. Last, but not least, thank you to my rock, Chris Hodgdon. I am truly grateful for everything he has done to allow me to undertake this seemingly endless process—including bravely and enthusiastically packing his bags to travel to Zimbabwe and Missouri, among other places.

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ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

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I always had a fondness for canids and other carnivores, but apparently after first learning of the existence of painted dog years ago, my path was inexplicably tied to them. Thank you to the following: Joe Greathouse (for providing the initial painted dog research ideas), Jane M. Packard (for supporting my first “dog” research project), my APD-SSP people: Mike Quick, Christina Gorsuch, and Dana Burke, the Endangered Wolf Center (EWC) team (Regina Mossotti, Erin Connett, Sarah Holaday, Rachel Crosby, Danielle Rosenstein, Kelsey Rumley, Tracy Rein, Erin Harms, and Brit Black), my EWC interns (Mackenzie Murphy, Kara Pohlman, Kristin Ranker, Mariah Whitmire, Zach Amir, Zack Larsen, Deanna Deterding, Maura Ryan, Jen Backer, Patrick Glass, Jack Luth, Kristin Ranker, Rebecca Kiesel, and Audrey Kocher), the Painted Dog Research Trust (PDRT) team, Dr. David Powell, and Denver Zoo, Oklahoma City Zoo, Rolling Hills Zoo, Chicago Zoological Society, Cincinnati Zoo, Audubon Zoo, Sedgwick County Zoo, Tulsa Zoo, Honolulu Zoo, Binder Park Zoo, Pueblo Zoological Society, Houston Zoo, and Kansas City Zoo for putting up with all my inquiries and dedicating themselves to the well-being of the animals (painted dogs and many other species) in their care.

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ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

Table of Contents

Abstract	iv
Acknowledgments.....	vi
Chapter I: Introduction.....	1
Anthropogenic Impacts on Wildlife.....	1
Reproductive Effects of Anthropogenic Disturbance on Wildlife	2
Focal Species: African Painted Dogs	4
Potential Direct and Indirect Anthropogenic Impacts to Painted Dogs	5
Dissertation Overview	7
References	10
Chapter II: #DigitalConservation: Using Social Media to Investigate the Scope of African Painted Dog (<i>Lycaon pictus</i>) Den Disturbance by Humans	19
Abstract	19
Introduction.....	20
Methods.....	23
Focal Species.....	23
Content Analysis	24
Data Collection.....	25
Results.....	27
Discussion	29
Use of Social Media and Content Analysis.....	29
Human Visits to Painted Dog Den Sites	30
Future Research.....	32
References.....	34
Chapter III: Quantitative Photogrammetric Methodology for Measuring Mammalian Belly Score in a Large Carnivore	41
Abstract	41
Introduction.....	43
Body Condition Scoring.....	43
Quantitative vs. Visual Estimation.....	46
Example of Quantitative Belly Score Measurements	47
Methods.....	49

ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

Study Area.....	49
Focal Species.....	50
Data Collection.....	51
Image Processing.....	51
Interrater Reliability	52
Data Analysis	57
Results.....	59
Discussion	61
Management Implications.....	62
References.....	65
Chapter IV: Do Human-Created Trails Influence the Presence of African Carnivores and Herbivores?	74
Abstract.....	74
Introduction.....	76
Methods.....	80
Study Area.....	80
Identification of Potential Modified and Unmodified Trail Sites	81
Modified and Unmodified Trails.....	82
Data Processing.....	85
Data Analysis	86
Carnivore and Herbivore Trail Usage	86
Latent Time to First Detection.....	86
Time of Day Species Observed	86
Characterization of Mammalian Community	87
Results.....	88
Carnivore and Herbivore Trail Usage	88
Latent Time to First Detection	88
Time of Day Species Observed.....	88
Characterization of Mammalian Community.....	89
Discussion	91
References.....	97

ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

Chapter V: Feeding Regimen and Growth Comparison in Two Related African Painted Dog (<i>Lycaon pictus</i>) Litters	106
Abstract	106
Introduction	107
Methods	111
Study Site	111
Litters	111
Enclosures	111
Diet	112
Litter A Feeding Protocol	113
Litter B Feeding Protocol	114
Data Collection	114
Wellness checks	114
Morphometric measurements	115
Data Analysis	116
Morphometric measurements	116
Results	118
Discussion	124
References	129
Chapter VI: Conclusion	134
Future Research & Management Recommendations	139
References	145
Appendix A: Permissions	150

ANTHROPOGENIC IMPACTS ON LYCAON PICTUS

List of Tables

Table 3-1. Definitions of morphometric terms used to calculate relative belly score for <i>Lycaon pictus</i>	53
Table 3-2. Formulas used in Excel spreadsheet to derive belly scores for <i>Lycaon pictus</i> from morphometric measurements	54
Table 3-3. Example of Excel spreadsheet for morphometric measurement data entry. Formulas to calculate belly scores for <i>Lycaon pictus</i> from these measurements are pre-entered into the appropriate cells	55
Table 3-4. Summary statistics of <i>Lycaon pictus</i> belly score means in Hwange and Mana Pool regions from suitable photographs obtained from 2004–2015	60
Table 4-1. All mammalian and avian species identified on camera traps on modified and unmodified trails from 32 sites collected over 2,996 trap nights.....	90
Table 5-1. Definitions of morphometric measurements obtained for each painted dog pup at 10 and 14-week wellness checks at the Endangered Wolf Center.....	116
Table 5-2. Morphometric measurement definitions for three of five response variables used in analyses of <i>Lycaon pictus</i> belly scores	117
Table 5-3. Comparison of morphometric means and weights between painted dog Litter A and Litter B at 10 and 14-week pup wellness checks and results of the fixed effects from the mixed effects models	118
Table 5-4. Comparison of mean weights (in grams) between captive painted dog Litter A and Litter B at 53 and 49 days of age, respectively, and mean weights of North American captive litters born between 1994 and 2017 (total of 503 individuals)	123

List of Figures

Figure 2-1. Areas of painted dog den visits documented by humans on social media.	28
Figure 3-1. Example of suitable photograph of painted dog (<i>Lycaon pictus</i>) showing front leg (FL), belly chord length (BCL) and belly depth (BD) measurements and leg angle (denoted by Θ) used to obtain belly score	56
Figure 3-2. African painted dog (<i>Lycaon pictus</i>) skeletal structure demonstrating floating ribs and discrete points from which morphometric measurements to calculate belly score were derived.....	57
Figure 3-3. Monthly variation in <i>Lycaon pictus</i> belly score means between the Hwange and Mana Pools regions, Zimbabwe.....	60
Figure 4-1. Hwange-Matetsi Complex study site in northwestern Zimbabwe.	81
Figure 4-2. Modified trail (i.e., existing game trail that was cleared and/or widened).....	83
Figure 4-3. Unmodified trail (i.e., existing game trail that was unaltered and used as a control)84	
Figure 4-4. Summary of time of day carnivores and herbivores were observed using trails.....	89
Figure 5-2. Morphometric measurements obtained for each painted dog pup during 10 and ... 14-week wellness checks at the Endangered Wolf Center..	115
Figure 5-3. Interaction plot comparing painted dog pup means of HL/BL (ratio of THL [total hind leg] divided by BL [body length]) between Litter A (free feed) and Litter B (controlled feed) at 10 and 14-week pup wellness checks	120
Figure 5-4. Interaction plot comparing painted dog pup means of FL-HL/BL (difference between TFL [total front leg] and THL [total hind leg] divided by BL [body length]) between Litter A (free feed) and Litter B (controlled feed) at 10 and 14-week pup wellness checks.....	121
Figure 5-5. Comparison of painted dog pup body and limb lengths based on morphometric measurements obtained from Litter A (on left; free feed) and Litter B (on right; controlled feed) at 10-week pup wellness check.....	122
Figure 5-6. Comparison of painted dog pup body and limb lengths based on morphometric means obtained from Litter A (on left; free feed) and Litter B (on right; controlled) at 14-week pup wellness check.	122

Chapter I: Introduction Anthropogenic Impacts on Wildlife

Consumptive (e.g., hunting and fishing) and non-consumptive (e.g., hiking and wildlife viewing) activities present a threat to wildlife (Müllner, Linsenmair, & Wikelski, 2004; Nortje, van Hoven, & Laker, 2012; Storch, 2013) through the disturbance or destruction of species, habitats, and ecosystems (Bentz, Lopes, Calado, & Dearden, 2016; Isaacs, 2000). This can lead to detrimental consequences for both the livelihoods of those who provide recreational opportunities and the natural resources themselves. Human activity in the form of tourism and other recreational activities has been shown to influence fitness in multiple species by altering diel activity (Corcoran et al., 2013), foraging behaviors (Dunn, Hamer, & Benton, 2010), and immune responses (French, DeNardo, Greives, Strand, & Demas, 2010) at local and landscape levels (Suraci, Clinchy, Zanette, & Wilmers, 2019). This is concerning as wildlife related tourism is ranked as a top attraction worldwide (World Tourism Organization, 2014); directly and indirectly generating over \$300 billion to global economies in 2018 alone (World Travel & Tourism Council, 2019).

Tourist expectations of close encounters with nature (Reynolds & Braithwaite, 2001) can incentivize tour guides and operators to meet these expectations regardless of the consequences to wildlife or the environment (Macdonald et al., 2017; Nortje et al., 2012; Reynolds & Braithwaite, 2001). A review of three tourism case studies evaluated the potential benefits and challenges these activities may have on the conservation of predators (big cats, crocodiles, and sharks; Macdonald et al., 2017). In the case of big cats, some tourists reported that they would engage in repeat visits until they saw the species they wanted to see (Macdonald et al., 2017). Others may be willing to go to additional lengths to get close encounters. This includes supplemental feedings for wildlife and crowds of vehicles that surround an individual or group of

animals (Macdonald et al., 2017), all of which may adversely affect wildlife (referred to as anthropogenic disturbance or impacts; Berger-Tal & Saltz, 2019).

Reproductive Effects of Anthropogenic Disturbance on Wildlife

Anthropogenic impacts to wildlife may be stronger when risks to animals are greater, such as during vulnerable periods when animals are raising young (Frid & Dill, 2002; Müllner et al., 2004; Sazatornil et al., 2016). Altered behavior and activity patterns may lead to negative consequences to both adult and young fitness and survival. Christiansen, Lusseau, Stensland, & Berggren (2010) noted that physiological stress increases energy costs and decreases energy reserves in multiple species. For example, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were less likely to forage, socialize, or rest in the presence of tourists. As females nurse their calves while resting, less rest may affect calf survival (Christiansen et al., 2010) as well as mother-calf interactions. Female barn owls (*Tyto alba*) began sleeping outside of nest boxes sooner in boxes frequently visited by humans, possibly affecting both feeding and thermoregulation of young (Almasi, Beziers, Roulin, & Jenni, 2015). Pronghorn antelope (*Antilocapra americana*) increased vigilance and decreased foraging behavior when in close proximity to roads with both low and high levels of traffic, particularly when young were present (Gavin & Komers, 2006). Hoatzin (*Opisthocomus hoazin*) chicks demonstrated higher levels of mortality at tourist visited sites compared to undisturbed nest sites, and juvenile hoatzins at undisturbed sites had significantly higher body weights than those at tourist visited sites (Müllner et al., 2004). Decreased rates of den attendance by spotted hyena (*Crocuta crocuta*) mothers were observed in areas with an increase in human activity (Greenberg & Holekamp, 2017), potentially leaving young exposed to predators and decreased feedings. In relation to increasing levels of human exposure, average and maximum reproductive rates decreased in California sea lions (*Zalophus californianus*; French, Gonzalez-Suarez, Young, Durham, & Gerber, 2011), and

cheetah (*Acinonyx jubatus*) cub recruitment was negatively affected (Broekhuis, 2018). These detrimental effects may also apply to African painted dogs.

African painted dogs (*Lycaon pictus*), also known as African wild dogs, painted wolves, and Cape hunting dogs, are one of Africa's most endangered carnivores. Their historical range included most of sub-Saharan Africa, but they currently exist in small, fragmented populations in eastern and southern Africa (Campana et al., 2016; Masenga et al., 2015; Range Wide Conservation Program for Cheetah & African Wild Dogs [RWCP], 2019). Anthropogenic activities such as persecution, snares, pathogens introduced via domestic dogs, and habitat fragmentation play direct and indirect roles in the painted dog's decline (Campana et al., 2016; Edwards, Rasmussen, Riordan, Courchamp, & Macdonald, 2013; Marsden et al., 2012; Woodroffe et al., 2007). Effects of these human-related activities include changes in morphology (Edwards et al., 2013), decreased genetic diversity (Marsden et al., 2012), decreased pack sizes (Courchamp, Rasmussen, & Macdonald, 2002), and Allee effects from low densities and fragmented populations (Angulo, Rasmussen, Macdonald, & Courchamp, 2013; Courchamp et al., 2006). As a highly social species, painted dogs are particularly vulnerable to the consequences of these types of negative effects (Rasmussen, Gusset, Courchamp, & Macdonald, 2008).

Human disturbance, primarily via tourism, may provide additional challenges (RWCP & IUCN/SSC, 2015). Despite the appearance of tolerance, den disturbance may lead to increased mortality due to den moves or interspecific predator presence (Lindsey, Alexander, du Toit, & Mills, 2005). The aim of this research was to explore these potential challenges. Following an overview of anthropogenic impacts on wildlife in general, I offer an introduction to my focal species, painted dogs. I then explore how tourism related activities (e.g., social media posts and

creation/use of recreational trails) may directly or indirectly impact free-ranging painted dogs during their denning season and offer a “quick” assessment method for monitoring the health of both free-ranging and zoological (i.e., captive) populations. In addition, I compare feeding regimens and growth in two related zoological litters of painted dogs to evaluate the effects of human care on individuals, with potential implications for free-ranging populations.

Focal Species: African Painted Dogs

Nomadic for most of the year, painted dogs are stationary for the approximately 12-week denning season. Energetic costs are extreme during this time due to the need to raise pups and become nomadic again (Rasmussen et al., 2008). Tour guides and operators may take advantage of this normally elusive species remaining in one area to offer clients the unique experience of observing both adults and pups. Gusset et al. (2008) noted that tourists responded positively to painted dogs, rated them as a top attraction, and were willing to pay extra to see them, potentially encouraging tour operators to expend additional efforts to locate dens. However, painted dogs have been heavily persecuted and extirpated from much of their historical range and typically avoid areas of human activity (Childes, 1988; Creel & Creel, 2002; Fanshawe, Frame, & Ginsberg, 1991; Woodroffe & Sillero-Zubiri, 2012). It has been suggested that human disturbance may be occurring during the most critical time in a painted dog’s life, interfering with painted dog foraging and social behaviors and contributing to higher mortality due to increased interspecific predator (e.g., lions [*Panthera leo*] and spotted hyenas) presence and den moves (Lindsey et al., 2005; Rasmussen & Macdonald, 2012).

If tourist activity at painted dog den sites is indeed negatively affecting painted dogs, this is a concern for stakeholders that include wildlife managers, policy makers, and landowners, and the species itself. In addition to the painted dog’s intrinsic and ecological value, reducing the reproductive success of an endangered species will have population implications in light of their

high energetic reproductive costs (particularly for packs with less than five individuals; Rasmussen et al., 2008). In addition, the loss or decline of a species that is valued by tourists can have further ecological and economic consequences.

Potential Direct and Indirect Anthropogenic Impacts to Painted Dogs

Among group-living carnivores, painted dogs have the highest known energetic costs of gestation (Creel & Creel, 2015; Gusset & Macdonald, 2010; Rasmussen et al., 2008). Costs are derived in part through the hunting and provisioning necessary to feed the lactating female and pups. Unborn pups are heavy in comparison to the female's body mass, and grow quickly, so females are "energetically in need of help during gestation and lactation" (Creel & Creel, 2002, p. 205). Capturing sufficient prey to feed all pack members while minimizing foraging costs is essential for painted dog reproductive success (Gusset & Macdonald, 2010; van der Meer, Mpofu, Rasmussen, & Fritz, 2013).

Humans may impose additional costs if their presence (regardless of intention) is perceived as a threat. The risk disturbance hypothesis proposes that non-lethal human disturbance is perceived by wildlife as similar to predation, and therefore, wildlife will exhibit tradeoff responses that reflect predation risk (Blumstein, Fernandez-Juricic, Zollner, & Garity, 2005; Frid & Dill, 2002; Gavin & Komers, 2006; Lowrey & Longshore, 2017; Peters & Otis, 2005). Tradeoff responses include increased vigilance, altered temporal and/or spatial patterns of habitat use to avoid humans (Corcoran et al., 2013; Rasmussen & Macdonald, 2012), diverted time and/or energy away from fitness related activities such as foraging and mating, or reduced parental care (and thus, reproductive success; Adamo & McKee, 2017; Blumstein et al., 2005, p. 944; Frid & Dill, 2002; Lowrey & Longshore, 2017; Storch, 2013).

Tradeoff responses leading to negative effects for painted dogs may be especially problematic if there is a steady flow of human activity at or near painted dog dens. Rode, Farley,

Fortin, and Robbins (2007) observed that adult male brown bears (*Ursus arctos*) decreased day foraging, and increased night foraging, in areas where human activity was experimentally introduced. Similarly, painted dogs may forego hunting and resting to assess each new approaching “threat,” affecting their ability to detect other threats as fatigue decreases the ability to remain vigilant (Brown et al., 2012; Cooper, Jr. & Blumstein, 2015). One painted dog pack with a den site consistently visited by humans demonstrated this temporal shift by engaging in more nocturnal hunting, which is typically performed at dawn and dusk, and decreasing overall activity at the den despite their highly social nature (Rasmussen & Macdonald, 2012). Pups were fed at various times during the night rather than in the morning and evening. Alteration of this pack’s activity reduced human encounters, but shifted “normal” resting, hunting, and feeding periods, which may have short or long-term consequences for these individuals (Rasmussen & Macdonald, 2012).

In addition to altering the timing of their activities, wildlife may avoid areas where humans are present. This can result in temporarily or permanently relocating to suboptimal habitats where predators or interspecific competitors are present. Painted dogs naturally occur at low densities (Creel & Creel, 2015; Davies-Mostert, Mills, & Macdonald, 2015; van der Meer et al., 2013) and will attempt to avoid lions and spotted hyenas due to interspecific killing and kleptoparasitism (Davies, Marneweck, Druce, & Asner, 2016; Davies-Mostert et al., 2015; Jackson et al., 2014; Rasmussen & Macdonald, 2012; van der Meer et al., 2013). If humans are perceived as a predation risk by painted dogs, and their presence precipitates increased den moves to avoid humans or altered foraging behavior from crepuscular to night, this may increase the risk of interactions with interspecific competitors.

Painted dogs could face additional indirect anthropogenic impacts as well. Optimal foraging theory predicts that animals will allocate their time and energy in the most economical manner when searching for and obtaining food resources (Fortin et al., 2015, MacArthur & Pianka, 1966). A stable prey base within close range of a den decreases the amount of search and pursuit time, and hence, energy expenditure. However, human presence may affect if, and how long, a pack remains at a den site with sufficient prey. Packs must decide whether current energetic costs and benefits are worth risking the presence of humans, or if they should relocate, resulting in more energy expended during the move and additional energy needed to hunt prey species.

Dissertation Overview

With energetic costs and pup mortality rates already high during denning season (Creel & Creel, 2015; Gusset & Macdonald, 2010; Jackson et al., 2014; Rasmussen et al., 2008), human disturbance may impose additional costs and risks. Multiple methods (e.g., content analysis, photogrammetry, camera traps) were incorporated into this research to investigate potential direct and indirect effects of anthropogenic activities on free-ranging painted dog packs in Zimbabwe and two zoological litters of painted dogs in the United States. My aim was to explore how human activities may influence painted dog behavior and fitness during the vulnerable period when they are raising young. This was done through the following: (a) identifying locations where painted dog dens have been visited by humans; (b) developing and using a belly score method as a means of comparing body condition between/among individuals and populations; (c) investigating how human-modified trails may influence the presence of carnivores and herbivores, thereby indirectly impacting painted dog fitness and survival; and (d) comparing feeding regimens (i.e., free feed and controlled feed) and growth of two zoological painted dog litters.

I demonstrate the use of social media as a conservation tool in Chapter II. Before investigating effects of human activity at painted dog dens, it was important to identify whether this activity was occurring, and if so, whether it was concentrated or widespread. Through publicly posted images and captions, I identified where humans stated they had visited painted dog dens. This provided a baseline of data that indicated this activity occurred in at least half of the countries where painted dogs are known to exist.

A second conservation tool is introduced in Chapter III. The development and use of a belly score measurement method allowed for a body condition comparison between two populations of painted dogs (Hwange National Park and Mana Pools National Park, Zimbabwe). This tool provides an option for a quick, noninvasive assessment of individuals, and potentially populations, of painted dogs (or other species of concern) that may offer an indicator of foraging success. It can also be used as a tool to compare body condition and fitness among individual painted dogs that reside at zoological facilities.

In Chapter IV, I examine a potential indirect effect of human activity at painted dog dens through the creation of trails by humans. Human disturbance of wildlife takes various forms, and one may involve humans unintentionally attracting interspecific predators (i.e., lions and hyenas) to painted dog dens, creating an additional threat of injury or death to painted dogs. To test the hypothesis that these predators may follow human tracks to painted dog dens, new trails were created and monitored for carnivore and herbivore presence.

Chapter V switches focus from free-ranging packs in Zimbabwe to two captive painted dog litters at a North American conservation center. More information is needed to improve husbandry practices, particularly for animals targeted for reintroduction or those considered to be genetically valuable. Humans can unintentionally and indirectly influence the growth of

individuals under their care (Canington, Sylvester, Burgess, Junno, & Ruff., 2018; Curtis, Orke, Tetradis, & van Valkenburgh, 2018; Kamaluddin, Tanaka, Wakamori, Nishimura, & Ito., 2019; Wisely et al., 2005). Here I explore how two feeding regimens (i.e., free and controlled feed) may affect growth in painted dogs, with implications for free-ranging populations under food stress.

Finally, Chapter VI provides an overview of the findings. Suggestions for future research and management considerations are included.

References

- Adamo, S. A., & McKee, R. (2017). Differential effects of predator cues versus activation of fight-or-flight behaviour on reproduction in the cricket *Gryllus texensis*. *Animal Behaviour*, 134, 1–8. <https://doi.org/10.1016/j.anbehav.2017.09.027>
- Almasi, B., Beziers, P., Roulin, A., & Jenni, L. (2015). Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. *Oecologia*, 179(1), 89–101. <https://doi.org/10.1007/s00442-015-3318-2>
- Angulo, E., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2013). Do social groups prevent Allee effect related extinctions? The case of wild dogs. *Frontiers in Zoology*, 10(11), 1–13. <https://doi.org/10.1186/1742-9994-10-11>
- Bentz, J., Lopes, F., Calado, H., & Dearden, P. (2016). Sustaining marine wildlife tourism through linking Limits of Acceptable Change and zoning in the Wildlife Tourism Model. *Marine Policy*, 68, 100–107. <https://doi.org/10.1016/j.marpol.2016.02.016>
- Berger-Tal, O. & Saltz, D. (2019). Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation. *Philosophical Transactions Royal Society B*, 374: 20180049. <https://doi.org/10.1098/rstb.2018.0049>
- Blumstein, D. T., Fernandez-Juricic, E., Zollner, P. A., & Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, 42(5), 943–953. <https://doi.org/10.1111/j.1365-2664.2005.01071.x>
- Broekhuis, F. (2018). Natural and anthropogenic drivers of cub recruitment in a large carnivore. *Ecology and Evolution*, 8(13), 1–8. <https://doi.org/10.1002/ece3.4180>

- Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. *PLoS ONE*, 7(7). <https://doi.org/10.1371/journal.pone.0040505>
- Campana, M. G., Parker, L. D., Hawkins, M. T. R., Young, H. S., Helgen, K. M., Gunther, M. S., . . . Fleischer, R. C. (2016). Genome sequence, population history, and pelage genetics of the endangered African wild dog (*Lycaon pictus*). *BMC Genomics*, 17. <https://doi.org/10.1186/s12864-016-3368-9>
- Canington, S. L., Sylvester, A. D., Burgess, M. L., Junno, J-A., & Ruff, C. B. (2018). Long bone diaphyseal shape follows different ontogenetic trajectories in captive and wild gorillas. *American Journal of Physical Anthropology*, 167(2), 366–376. <https://doi.org/10.1002/ajpa.23636>
- Childes, S. L. (1988). The past history, present status and distribution of the hunting dog *Lycaon pictus* in Zimbabwe. *Biological Conservation*, 44(4), 301–316. [https://doi.org/10.1016/0006-3207\(88\)90022-5](https://doi.org/10.1016/0006-3207(88)90022-5)
- Christiansen, F., Lusseau, D., Stensland, E., & Berggren, P. (2010). Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endangered Species Research*, 11, 91–99. <https://doi.org/10.3354/esr00265>
- Cooper, Jr., W. E., & Blumstein, D. T. (Eds.). (2015). *Escaping from Predators: An Integrative View of Escape Decisions*. United Kingdom: Cambridge University Press.
- Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., & Harvey, G. M. (2013). Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the Southern stingray, *Dasyatis americana*. *PLoS ONE*, 8(3): e59235. <https://doi.org/10.1371/journal.pone.0059235>

- Courchamp, F., & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation*, 4, 169–174.
<https://doi.org/10.1017/S1367943001001196>
- Courchamp, F., Rasmussen, G. S. A., & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13(1), 20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006). Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biology*, 4(12): e415. <https://doi.org/10.1371/journal.pbio.0040415>
- Creel, S., & Creel, N. M. (2015). Opposing effects of group size on reproduction and survival in African wild dogs. *Behavioral Ecology*, 26(5), 1414–1422.
<https://doi.org/10.1093/beheco/arv100>
- Creel, S., & Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton, NJ: Princeton University Press.
- Curtis, A. A., Orke, M., Tetradis, S., & van Valkenburgh, B. (2018). Diet-related differences in craniodental morphology between captive-reared and wild coyotes, *Canis latrans* (Carnivora: Canidae). *Biological Journal of the Linnean Society*, 123, 677–693.
<https://doi.org/10.1093/biolinnean/blx161>
- Davies-Mostert, H. T., Mills, M. G. L., & Macdonald, D. W. (2015). The demography and dynamics of an expanding, managed African wild dog metapopulation. *African Journal of Wildlife Research*, 45(2), 258–273. <https://doi.org/10.3957/056.045.0258>

- Davies, A. B., Marneweck, D. G., Druce, D. J., & Asner, G. P. (2016). Den site selection, pack composition, and reproductive success in endangered African wild dogs. *Behavioral Ecology*, 27(6), 1869–1879. <https://doi.org/10.1093/beheco/arw124>
- Dunn, J. C., Hamer, K. C., & Benton, T. G. (2010). Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. *Journal of Applied Ecology*, 47(5), 994–1002. <https://doi.org/10.1111/j.1365-2664.2010.01856.x>
- Edwards, C. T. T., Rasmussen, G. S. A., Riordan, P., Courchamp, F., & Macdonald, D. W. (2013). Non-adaptive phenotypic evolution of the endangered carnivore *Lycaon pictus*. *PLoS ONE*, 8(9): e73856. <https://doi.org/10.1371/journal.pone.0073856>
- Fanshawe, J. H., Frame, L. H., & Ginsberg, J. R. (1991). The wild dog—Africa's vanishing carnivore. *Oryx*, 25(3), 137–146. <https://doi.org/10.1017/S0030605300034165>
- Fortin, D., Merkle, J. A., Sigaud, M., Cherry, S. G., Plante, S., Drolet, A., & Labrecque, M. (2015). Temporal dynamics in the foraging decisions of large herbivores. *Animal Production Science*, 55, 376–383. <https://doi.org/10.1071/AN14428>
- French S. S., DeNardo, D. F., Greives, T. J., Strand, C. R., & Demas, G. E. (2010). Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior*, 58(5), 792–799. <https://doi.org/10.1016/j.yhbeh.2010.08.001>
- French, S. S., Gonzalez-Suarez, M., Young, J. K., Durham, S., & Gerber, L. R. (2011). Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PLoS ONE*, 6(3). <https://doi.org/10.1371/journal.pone.0017686>

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk.

Conservation Ecology, 6(1). <http://www.consecol.org/vol6/iss1/art11/>

Gavin, S. D., & Komers, P. E. (2006). Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology*, 84(12), 1775–1780.

<https://doi.org/10.1139/z06-175>

Greenberg, J. R., & Holekamp, K. E. (2017). Human disturbance affects personality development in a wild carnivore. *Animal Behaviour*, 132, 303–312.

<https://doi.org/10.1016/j.anbehav.2017.08.023>

Gusset, M., & Macdonald, D.W. (2010). Group size effects in cooperatively breeding African wild dogs. *Animal Behaviour*, 79, 425–428.

<https://doi.org/10.1016/j.anbehav.2009.11.021>

Gusset, M., Maddock, A. H., Gunther, G. J., Szykman, M., Slotow, R., Walters, M., & Somers, M. J. (2008). Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation*, 17(1), 83–101.

<https://doi.org/10.1007/s10531-007-9232-0>

Isaacs, J. C. (2000). The limited potential of ecotourism to contribute to wildlife conservation.

Wildlife Society Bulletin, 28(1), 61–69. <https://doi.org/10.2307/4617284>

Jackson, C. R., Power, R. J., Groom, R. J., Masenga, E. H., Mjingo, E. E., Fyumagwa, R. D., Roskaft, E., & Davies-Mostert, H. (2014). Heading for the hills: risk avoidance drives den site selection in African wild dogs. *PLoS ONE*, 9(6).

<https://doi.org/10.1371/journal.pone.0099686>

- Kamaluddin, S. N., Tanaka, M., Wakamori, H., Nishimura, T., & Ito, T. (2019). Phenotypic plasticity in the mandibular morphology of Japanese macaques: captive-wild comparison. *Royal Society Open Science*, 6, 181382. <https://doi.org/10.1098/rsos.181382>
- Lindsey, P. A., Alexander, R. R., du Toit, J. T., & Mills, M. G. L. (2005). The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biological Conservation*, 123, 339–348. <https://doi.org/10.1016/j.biocon.2004.12.002>
- Lowrey, C., & Longshore, K. M. (2017). Tolerance to disturbance regulated by attractiveness of resources: a case study of desert bighorn sheep within the River Mountains, Nevada. *Western North American Naturalist*, 77(1), 82–98. <https://doi.org/10.3398/064.077.0109>
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603–609.
- Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., & Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biological Conservation*, 215, 132–141. <https://doi.org/10.1016/j.biocon.2017.07.013>
- Marsden, C. D., Woodroffe, R., Mills, M. G. L., McNutt, J. W., Creel, S., Groom, R., ... Mable, B. K. (2012). Spatial and temporal patterns of neutral and adaptive genetic variation in the endangered African wild dog (*Lycaon pictus*). *Molecular Ecology*, 21(6), 1379–1393. <https://doi.org/10.1111/j.1365-294X.2012.05477.x>
- Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., ... Røskaft, E. (2015). Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, 54(1), 95–98. <https://doi.org/10.1111/aje.12244>

- Müllner, A., Linsenmair, K. E., & Wikelski, M. (2004). Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, 118, 549–558. <https://doi.org/10.1016/j.biocon.2003.10.003>
- Nortje, G. P., van Hoven, W., & Laker, M. C. (2012). Factors affecting the impact of off-road driving on soils in an area in the Kruger National Park, South Africa. *Environmental Management*, 50(6), 1164–1176. <https://doi.org/10.1007/s00267-012-9954-y>
- Peters, K. A., & Otis, D. L. (2005). Using the risk-disturbance hypothesis to assess the relative effects of human disturbance and predation risk on foraging American oystercatchers. *The Condor*, 107(3), 716–725. <https://doi.org/10.1093/condor/107.3.716>
- Range Wide Conservation Program for Cheetah & African Wild Dogs (RWCP). (2019). *Range Wide Conservation Program for Cheetah & African Wild Dog*. Retrieved from <http://www.cheetahandwilddog.org/>
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D.W. (2008). Achilles heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. <https://doi.org/10.1086/590965>
- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286(3), 232–242. <https://doi.org/10.1111/j.1469-7998.2011.00874.x>
- Reynolds, P. C., & Braithwaite, D. (2001). Towards a conceptual framework for wildlife tourism. *Tourism Management*, 22(1), 31–42. [https://doi.org/10.1016/S0261-5177\(00\)00018-2](https://doi.org/10.1016/S0261-5177(00)00018-2)

- Rode, K. D., Farley, S. D., Fortin, J., & Robbins, C. T. (2007). Nutritional consequences of experimentally introduced tourism in brown bears. *Journal of Wildlife Management*, 71(3), 929–939. <https://doi.org/10.2193/2006-075>
- RWCP & IUCN/SSC 2015. *Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa*; Revised and Updated, August 2015.
- Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., ... López-Bao, J.V. (2016). The role of human-related risk in breeding site selection by wolves. *Biological Conservation*, 201, 103–110. <https://doi.org/10.1016/j.biocon.2016.06.022>
- Storch, I. (2013). Human disturbance of grouse—why and when? *Wildlife Biology*, 19(4), 390–403. <https://doi.org/10.2981/13-006>
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22, 1578–1586. <https://doi.org/10.1111/ele.13344>
- van der Meer, E., Mpofu, J., Rasmussen, G. S. A., & Fritz, H. (2013). Characteristics of African wild dog natal dens selected under different interspecific predation pressures. *Mammalian Biology*, 78(5), 336–343. <https://doi.org/10.1016/j.mambio.2013.04.006>
- Wisely, S. M., Santymire, R. M., Livieri, T. M., Marinari, P. E., Kreeger, J. S., Wildt, D. E., & Howard, J. G. (2005). Environment influences morphology and development for *in situ* and *ex situ* populations of the black-footed ferret (*Mustela nigripes*). *Animal Conservation*, 8, 321–328. <https://doi.org/10.1017/S1367943005002283>
- Woodroffe, R., Davies-Mostert, H., Ginsberg, J., Graf, J., Leigh, K., McCreery, K., ... Szykman, M. (2007). Rates and causes of mortality in Endangered African wild dogs

Lycaon pictus: Lessons for management and monitoring. *Oryx*, 41(2), 215–223.

<https://doi.org/10.1017/s0030605307001809>

Woodroffe, R., & Sillero-Zubiri, C. (2012). *Lycaon pictus*. The IUCN Red List of Threatened Species 2012: e.T12436A16711116.

<https://doi.org/10.2305/IUCN.UK.2012.RLTS.T12436A16711116.en>

World Tourism Organization. (2014). *Towards measuring the economic value of wildlife watching tourism in Africa: briefing paper*. Madrid: World Tourism Organization.

World Travel & Tourism Council. (2019). *The Economic Impact of Global Wildlife Tourism. Travel & Tourism as an Economic Tool for the Protection of Wildlife - August 2019*.

Retrieved from <https://travesiasdigital.com/wp-content/uploads/2019/08/The-Economic-Impact-of-Global-Wildlife-Tourism-Final-19.pdf>

Chapter II: #DigitalConservation: Using Social Media to Investigate the Scope of African Painted Dog (*Lycaon pictus*) Den Disturbance by Humans

Abstract

Social media platforms allow people to share experiences, thoughts, and actions through words and images, including human interactions with both domestic and wild animals.

Human-wildlife interactions have been documented to have negative effects on wildlife, with implications for endangered species. Here I offer an example of the use of social media and a content analysis framework to identify general locations of a specific human-endangered wildlife interaction: human activity at painted dog (*Lycaon pictus*) den sites. Two hundred twenty images and captions relating to den visits were collected from four social media platforms, and then general den visit locations were mapped. Results indicate that den visits by humans occurred in seven of 14 countries where painted dogs are known to be present. This information provides a starting point for further investigation into the impacts of this activity on painted dogs, which is valuable to the effective management of human-caused disturbances (e.g., reducing potential anthropogenic Allee effects) for this species.

Keywords: human disturbance, anthropogenic impact, wildlife conservation, anthropogenic Allee effect, content analysis

Introduction

Social media (websites and applications like Facebook and Twitter) is an integral part of today's society. These user-generated content platforms allow people to share experiences, thoughts, and actions (Fidino et al., 2018), including interactions with other species (Eid & Handal, 2018; Toivonen et al., 2019). This can be both beneficial and detrimental to the animals and/or humans involved (Hausmann et al., 2018; Nghiem et al., 2012). Images of cute or abused animals posted to social media can raise awareness, garner fundraising support, or enable rescuers to find homes for animals in need. Unfortunately, geospatial data and/or easily identifiable landscape features within some images may also provide leads for poachers to locate commercially valuable species, including both charismatic fauna and those less well-known (Di Minin et al., 2015; Eid & Handal, 2018). This might result in more wildlife being tracked, captured, injured, and/or killed (Di Minin et al., 2018; Welz, 2017; Wu et al., 2018).

Despite these threats, images of species may also be beneficial for research and conservation. The term “digital conservation” was first used publicly in 2011 (van der Wal & Arts, 2015) and denotes an “emerging field of conservation science where digital technologies and novel data sources are being used to help stem biodiversity loss” (Hausmann et al., 2018, p. 1). Although currently not widely utilized, data from user-generated social media posts can provide an alternative or supplement to more traditional research methods such as field visits and in-person or online surveys, which can be costly and time-consuming. Uses for user-generated data include ecosystem and species mapping and monitoring (Kelling et al., 2015), tourist visitation preferences (Levin et al., 2015; Toivonen et al., 2019; Wood et al., 2013), and conservation communication, marketing, and education (Di Minin et al., 2015; Nghiem et al., 2012). When used in conjunction with content analysis, other perspectives and uses may emerge.

Information from websites has been used in a supplementary manner in wildlife-related research, but there has been limited use of content analysis (CA) relating to wildlife tourism (Cong et al., 2014). Di Minin et al. (2015) used Instagram photo data and content analysis for their study of invasive species, population trends, and other ecological processes in Kruger National Park, South Africa. CA has also been used in other natural resource studies such as exploring use of the phrase “human-wildlife conflict” (Peterson et al., 2010) and researching public opinions of wolves, coyotes, opossums, and raccoons (Fidino et al., 2018; Houston et al., 2010). Combining social media data and CA may also provide a tool for researching conservation issues, including anthropogenic impacts on wildlife. As with any emerging method or tool, digital conservation will experience growing pains; however, Fidino et al. (2018) argued that tapping into this vast resource can be worth it. Social media can have a significant influence on people’s actions (Nghiem et al., 2012), and wildlife viewing is no exception.

Wildlife viewing and other recreational activities can present a threat to wildlife (Bentz et al., 2016; Isaacs, 2000; Müllner et al., 2004; Storch, 2013) through various negative impacts such as altering diel activity and foraging behaviors (Corcoran et al., 2013; Dunn et al., 2010), affecting immune responses (French et al., 2010), lowering body mass of young (Almasi et al., 2015), or by decreasing recruitment (Broekhuis, 2018). Wildlife tourists often desire close encounters with nature, incentivizing tour operators to meet these expectations regardless of consequences to wildlife or the environment (Macdonald et al., 2017; Nortje et al., 2012; Reynolds & Braithwaite, 2001). To achieve a close encounter with a species, particularly those that are rare, tourists may engage in repeat visits, pay greater amounts of money, and go to extreme lengths (e.g., supplemental feedings), putting themselves and wildlife at risk (Courchamp et al., 2006; Macdonald et al., 2017; Reynolds & Braithwaite, 2001). This can

create an anthropogenic Allee effect, or a “paradox of value” (Courchamp et al., 2006, p. 2405).

The anthropogenic Allee effect occurs when rare species are overexploited for profit, due to their rarity, ultimately increasing their rarity and leading to extinction (Courchamp et al., 2006). This is detrimental not only to the wildlife itself, but also to human livelihoods dependent on facilitating these recreational opportunities, an important consideration given that wildlife-related tourism is ranked as a top attraction worldwide (World Tourism Organization, 2014).

Because different species respond differently to human activities, it is imperative that we investigate the specifics of how human disturbance impacts individual animals, populations, and ecosystems. For example, some wolves tolerate human activity near dens and young (Thiel et al., 1998), while others avoid human disturbances (Person & Russell, 2009; Sidorovich et al., 2017), particularly during denning season (Roffler et al., 2018). How human presence affects wildlife behavior and fitness may have implications for tourism and wildlife management practices, especially for endangered and threatened species. The purpose of this study was twofold: (a) to explore a data resource (social media) using a method (content analysis) that may assist with conservation-related issues, and (b) to validate the occurrence of a particular human-wildlife interaction, human visitations to *Lycaon pictus* den sites, and map where den visits occurred.

Methods

Focal Species

The painted dog (*Lycaon pictus*, also known as the African wild dog) is one of Africa's most endangered carnivores. Historically found throughout sub-Saharan Africa, they currently exist in small, fragmented populations in eastern and southern Africa (RWCP, 2019).

Anthropogenic impacts such as persecution, snares, and habitat fragmentation contribute to the decline of this highly social species (Rasmussen, 2009; Woodroffe et al., 2007). These impacts include changes in morphology (Edwards et al., 2013) and activity patterns (Rasmussen & Macdonald, 2012), decreased genetic diversity (Marsden et al., 2012), and reduced pack size (Courchamp et al., 2002). Ironically, though historically declared vermin and shot on sight (Childes, 1988), the painted dog's rise in popularity as a "must see" animal on safaris highlights a potentially new and important concern: that they may well be victims of this anthropogenic Allee effect (Courchamp et al., 2006), and challenged with additional negative human impacts via tourism (RWCP & IUCN/SSC, 2015).

Nomadic and elusive for most of the year, painted dogs are fairly stationary for the approximately 12-week denning season, and all pack members participate in raising pups (Angulo et al., 2013; Courchamp et al., 2002; Rasmussen et al., 2008). Tour guides and operators take advantage of this fact to offer clients the unique experience of observing both adults and pups at a den. As Gusset et al. (2008) noted, tourists in South Africa responded positively to painted dogs, rated them as a top attraction, and were willing to pay extra to see them, all of which reinforces the potential for a tourism threat. Painted dogs however typically avoid areas of human activity, so human presence at den sites may have detrimental consequences including interfering with foraging and social behaviors, and the stress of moving dens (Rasmussen & Macdonald, 2012) while also trying to protect pups.

Because the scope of painted dog den visits by humans is unknown, if tourist activity at dens is indeed negatively affecting painted dog populations, this is a concern for the species, and also wildlife managers and other stakeholders connected to the well-being of these populations. Intrinsic value aside, a reduction in reproductive success of this endangered species can have further ecological consequences (Rasmussen et al., 2008).

Content Analysis

Content analysis (CA) is commonly used in the social and health sciences (Elo & Kyngäs, 2008; Hsieh & Shannon, 2005; Stepchenkova et al., 2009), as well as the communication, journalism, and business fields (Elo & Kyngäs, 2008; Neuendorf, 2017). As with many methods, CA lacks “firm definition and procedures,” and a researcher’s approach to CA depends on the research focus (Hsieh & Shannon, 2005, p. 1277). Hsieh and Shannon (2005) briefly defined three approaches: *Conventional* CA is generally used when there is limited literature or theory relating to a phenomenon. *Directed* CA is used for validation of an existing framework or theory, or to conceptually extend it. Finally, *Summative* CA uses interpretation to explore the usage of specific content (e.g., words or phrases).

Although Hsieh and Shannon’s (2005) definitions may be more applicable to the health and social science fields, their explanations were helpful in forming our own framework and approach for conservation work. Hence, we used the combined framework and definitions of directed and summative CA to validate the occurrence and general locations of human visits to painted dog dens and explore how social media data could be collected and analyzed to assess potential effects of den visitation by humans on painted dog reproductive fitness. For the purposes of this study, the general term, “framework,” refers to how the CA approaches and studies that utilized them were used as references, rather than how the specific phrases or words were analyzed. As stated by Neuendorf (2017), “content analysis uses messages . . . as its units

of data collection and analysis” (p. 36). While we required image captions to contain specific information, the words and phrases themselves were not analyzed, although that could potentially be explored in future studies.

Data Collection

Following Wood et al.’s (2013) investigation of social media and CA to estimate visitation rates to popular global tourist sites, I searched Facebook, Flickr, Instagram, and Twitter using the following phrases (English only): “wild dog den,” “painted dog den,” “African painted dog,” “African wild dog,” “lycaon pictus,” “painted dog pups,” and “wild dog pups.” I recorded images containing at least one painted dog pup, with or without an adult present, where the pups were of den age (approximately 4–12 weeks). Each image had to contain a caption specifically referencing the image being obtained at a den site, such as: “We were lucky to be able to visit a den and the mother called out the puppies so we could see them;” or, “my tracker is amazing—he was the first to spot and locate these wild dogs straight to their den where we found pups.”

I recorded as much of the following information as possible for each image: (a) country, (b) area or region within the country, (c) tour operator, (d) date posted, and (e) associated caption. These data were then used to map the distribution of den visits, highlighting general areas within a country where people recorded their visit to a painted dog den. The search for images and captions meeting the criteria specified above was conducted between June–December 2018, with posting dates on the images ranging from 2008 to 2018. Duplicate photos were omitted before analysis and map creation, as were multiple photos taken by the same person that included the same data (date, location, etc.). All images were publicly accessible; I did not visit personal social media pages or interact with those who posted the images.

There are automated tools and programs that assist with data analysis, but due to the current lack of automated options for the purposes of this particular study, all searches, image and caption reviews, and data recording and analysis were conducted manually. Once a search phrase was entered within the social media platforms, all images returned were reviewed to identify if any contained pups of den age. For those meeting the criteria, associated captions were reviewed for references to the image being taken at a den site. If that information was stated, a screenshot of the image and its caption was copied and pasted into a Word document, and as much information as possible was recorded in an Excel spreadsheet. For cross referencing purposes, the images in the Word document were given the row number of the associated data in the Excel spreadsheet.

Results

Two hundred twenty images (from a rough estimate of 700+ images) that met the criteria above were collected from four social media platforms: 61 from Instagram, 61 from Facebook, 56 from Twitter, and 42 from Flickr. Based on image and caption data, den visits occurred in seven African countries between 2008–2018 (Figure 1), with the majority of images (n=116; 53%) stated to have been taken in South Africa, followed by Botswana (n=41; 18%). The remaining images consisted of: Zimbabwe (n=12), Kenya (n=8), Tanzania (n=5), Zambia (n=5), Namibia (n=3), and unknown locations (n=30). General locations of den visits were provided so as not to highlight specific tour operators, nor disclose den site locations.

We also reviewed whether den visits occurred on private or protected land. Forty-two locations were specifically identified throughout the seven countries. Of these 42 locations, six were national parks, and 31 were private game reserves.

Figure 2-1

Areas of painted dog den visits documented by humans on social media. Diamonds indicate the general locations of den visits, regardless of frequency or number of visits. Grey shaded areas are the estimated range of known resident painted dog populations as of 2016 (RWCP, 2019).



Discussion

Use of Social Media and Content Analysis

By obtaining information from social media to investigate human-wildlife interactions and contribute to evolving management practices in multiple sectors, this effort provides a good example of a “digital conservation” study (Hausmann et al., 2018; van der Wal & Arts, 2015). Using a combination of social media and content analysis, I introduced results that demonstrate the widespread occurrence of human visits to painted dog dens, which can now be used to begin discussions, assess actual impacts on denning success, and develop policies or regulations. While painted dogs were the focus here, this approach can be applied to other species as well.

Despite the “data deluge” that social media provides, not all data are created equal, which leads to other considerations (Kitchin, 2013, p. 264). Although the data (i.e., images and captions) used in this study were publicly accessible, privacy and ethics are still concerns. For example, the intent of this study was to use images to document that a specific human activity, people visiting painted dog dens, was occurring. Additional information relating to the people who posted the photos, specific geographical locations, and tour operators who offered this activity were available for some images. Yet sharing that type of information here undermines the goal of this study in that it can increase chances of harm or harassment (i.e., physical or online) to both humans who participated in den visits, and the painted dogs themselves.

Another consideration is the context in which data are produced/shared and analyzed (Kitchin, 2013, pp. 264–265). While unable to elaborate here on the pros and cons of using big data in general, and our approach in particular, for conservation purposes, Kitchin’s (2013) reminder that “Big data . . . are both a representation and a sample” is important (p. 265). Here we collected images that represented the occurrence of this activity in multiple countries, yet further research is needed to determine whether this activity is consistently occurring throughout

the painted dog's range, or is confined to more localized areas. Incorporating tourist demographics and the ability to access technology to share social media posts may offer additional insight.

Human Visits to Painted Dog Den Sites

Human visits to painted dog dens were documented in seven of the 14 countries where painted dog populations are known to persist, providing a glimpse of what may be the “tip of the iceberg” for a potential growing threat to this species. Only seven countries were reported in the images collected during this study, but it is expected that this activity has occurred, or is occurring, in other countries as well, particularly if it is a profitable activity for private landowners, the tourism industry, and other stakeholders. Thirty of the images collected did not report the country where the den visit occurred, potentially identifying additional locations. Regardless, I was able to map general areas within countries where painted dog den visits have been documented, thus drawing attention to this issue. What was beyond the scope of this study to assess, but is imperative to evaluate as these actions may have the greatest impacts, are the frequency at which each den site was visited; the number of human visitors per day, site, or season; the impacts of human presence on individuals and packs (i.e., changes in behaviors or activities); method of approach (e.g., by foot or vehicle); den visits on private land versus in protected areas, and how den visits may influence the behavior of other carnivore and herbivore species (Chapter IV), thereby instigating local and landscape level consequences.

The 220 usable images and captions I found may not appear as robust as the sample sizes of previous social media studies, such as 30,000 evaluative expressions about wolves (Houston et al., 2010) or 606 photographs related to illegal hunting (Eid & Handal, 2018). Still, these data offer evidence of the widespread occurrence of painted dog den visits by humans within an approximately ten-year period. In addition to the brief data collection timeframe, other factors

may have hindered sample size. Factors include adapting a commonly used analysis method from other fields to explore an as yet unexamined conservation issue via a novel data source, and exclusion criteria that required both images and specific wording within captions. As people had to view pups at a den, then take a photo and post it using key tag words to be included in this study, there are likely many more den visits that did not result in usable posts. An extended search for images and captions within and beyond the social media platforms used here, as well as other search words and phrases, could yield an increased sample size that is potentially more widespread.

Over half the images that met the data collection criteria were documented as having occurred in South Africa. This may represent the actual relative frequency of den visits, or may be the result of disparities in behavior or technology access among tourists in different areas. High den visitation rates in a few areas may also be the result of ease of access to these regions, tour operator availability, and the density of known painted dog denning sites. Locations beyond these findings may also have experienced den visits; however, these may have been less represented on social media possibly due to fewer den sightings, limited access to technology, and tourist demographics (Di Minin et al., 2015; Elo & Kyngäs 2008; Fidino et al., 2018; Hausmann et al., 2018; Toivenen et al., 2019; Zeng & Gerritsen, 2014). Based on personal communications with wildlife and conservation staff in South Africa, Botswana, and Zambia, human visits to painted dog dens were not cited as an issue of concern for those countries. This may be due to wildlife managers, biologists, and others not being aware of the activity and its potential impact, or not acknowledging or reporting it. Data from the tourism sector, such as visitor demographics, number of visitors to specific African countries, number of individuals

participating in wildlife-related activities, and tour operators who offer the experience of viewing painted dogs, may offer additional insight.

Future Research

The use of social media and content analysis enabled the exploration of a potential threat to painted dogs: identifying locations where humans visited dens. Captions such as “These adorable wild dog pups have emerged from the new den guides found” and “These pups had just come out of their den for the first time” raise concerns that den visits may put both painted dog adults and pups at risk, even if negative impacts are not immediately or directly observed. It also highlighted “hotspots” such as South Africa that require further investigation, including whether this activity occurs in a few select areas or throughout the country. This work raises essential considerations for future painted dog research and conservation, including direct and indirect effects of humans visiting dens on painted dogs themselves (i.e., fitness, survival, attracting predators) and whether tourists feel differently about visiting dens after being educated about potential risks to painted dogs. In addition, among locations that were specifically identified, the majority of den visits occurred on private game reserves. Several private game reserves are near or adjacent to national parks, the distributional limit for this species, which has implications for existing/proposed regulations related to tourism on both private and national park land.

The short and long-term consequences of humans visiting painted dogs is unknown. All too often, precautionary measures are either not implemented, or not implemented in a timely manner. In the case of painted dog management plans and policies, it may be prudent to consider employing “buffer zones” for observing painted dog dens in any country or, as with wolves in Yellowstone National Park, temporary closure of den site areas (Smith et al., 2019) sooner rather than later. In addition to buffer zones, restricting the number of vehicles and/or tourists per den per day and specifying one or two locations from which den observations may

take place at each den could be an acceptable compromise that allows humans to continue to participate in this activity while respecting the health and safety of an endangered species.

Additional collaboration and dialogue are recommended to obtain the perspectives of all stakeholders and participants at multiple levels (i.e., local to national) to assist in decisions for the management of this species.

The use of social media and content analysis enabled me to gather preliminary data on the distribution of painted dog den visits to initiate and guide conservation management strategies for one species. I strongly encourage further research to aid painted dog conservation, but also ask readers to consider how this approach may benefit other species. For example, social media data may offer an overview of the biodiversity in a specific region, assist in assessing the health and fitness of a species or population (Chapter III), or provide a timeline for the occurrence of events that may impact species of interest. As suggested by Di Minin et al. (2015), social media data may be helpful for investigating human behaviors that affect conservation, allowing for a more interdisciplinary approach to inform management decisions relating to predators, prey, habitats, and ecosystems alike.

References

- Almasi, B., Beziers, P., Roulin, A., & Jenni, L. (2015). Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. *Oecologia*, 179(1), 89–101.
<https://doi.org/10.1007/s00442-015-3318-2>
- Angulo, E., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2013). Do social groups prevent Allee effect related extinctions? The case of wild dogs. *Frontiers in Zoology*, 10(11), 1–13. <https://doi.org/10.1186/1742-9994-10-11>
- Bentz, J., Lopes, F., Calado, H., & Dearden, P. (2016). Sustaining marine wildlife tourism through linking Limits of Acceptable Change and zoning in the Wildlife Tourism Model. *Marine Policy*, 68, 100–107. <https://doi.org/10.1016/j.marpol.2016.02.016>
- Broekhuis, F. (2018). Natural and anthropogenic drivers of cub recruitment in a large carnivore. *Ecology and Evolution*, 8(13), 1–8. <https://doi.org/10.1002/ece3.4180>
- Childes, S. L. (1988). The past history, present status and distribution of the hunting dog *Lycaon pictus* in Zimbabwe. *Biological Conservation*, 44(4), 301–316.
[https://doi.org/10.1016/0006-3207\(88\)90022-5](https://doi.org/10.1016/0006-3207(88)90022-5)
- Cong, L., Wu, B., Morrison, A. M., Shu, H., & Wang, M. (2014). Analysis of wildlife tourism experiences with endangered species: an exploratory study of encounters with giant pandas in Chengdu, China. *Tourism Management*, 40, 300–310.
<https://doi.org/10.1016/j.tourman.2013.07.005>
- Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., & Harvey, G. M. (2013). Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the Southern stingray, *Dasyatis americana*. *PLoS ONE*, 8(3): e59235. <https://doi.org/10.1371/journal.pone.0059235>

- Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biology*, 4(12), e415. <https://doi.org/10.1371/journal.pbio.0040415>
- Courchamp, F., Rasmussen, G. S. A., & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13(1), 20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Di Minin, E., Fink, C., Hiippala, T., & Tenkanen, H. (2018). A framework for investigating illegal wildlife trade on social media with machine learning. *Conservation Biology*, 33(1), 210–213. <https://doi.org/10.1111/cobi.13104>
- Di Minin, E., Tenkanen, H., & Toivonen, T. (2015). Prospects and challenges for social media data in conservation science. *Frontiers in Environmental Science*, 3(63), 1–10. <https://doi.org/10.3389/fenvs.2015.00063>
- Dunn, J. C., Hamer, K. C., & Benton, T. G. (2010). Fear for the family has negative consequences: Indirect effects of nest predators on chick growth in a farmland bird. *Journal of Applied Ecology*, 47(5), 994–1002. <https://doi.org/10.1111/j.1365-2664.2010.01856.x>
- Edwards, C. T. T., Rasmussen, G. S. A., Riordan, P., Courchamp, F., & Macdonald, D. W. (2013). Non-adaptive phenotypic evolution of the endangered carnivore *Lycaon pictus*. *PLoS ONE*, 8(9): e73856 <https://doi.org/10.1371/journal.pone.0073856>
- Eid, E., & Handal, R. (2018). Illegal hunting in Jordan: Using social media to assess impacts on wildlife. *Oryx*, 52(4), 730–735. <https://doi.org/10.1017/S0030605316001629>
- Elo, S., & Kyngäs, H. (2008). The qualitative content analysis process. *The Journal of Advanced Nursing*, 62(1), 107–115. <https://doi.org/10.1111/j.1365-2648.2007.04569.x>

- Fidino, M., Herr, S. W., & Magle, S. B. (2018). Assessing online opinions of wildlife through social media. *Human Dimensions of Wildlife*, 23(5), 482–490.
<https://doi.org/10.1080/10871209.2018.1468943>
- French S. S., DeNardo, D. F., Greives, T. J., Strand, C. R., & Demas, G. E. (2010). Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior*, 58(5), 792–799.
<https://doi.org/10.1016/j.yhbeh.2010.08.001>
- Gusset, M., Maddock, A. H., Gunther, G. J., Szykman, M., Slotow, R., Walters, M., & Somers, M. J. (2008). Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation*, 17(1), 83–101.
<https://doi.org/10.1007/s10531-007-9232-0>
- Hausmann, A., Toivonen, T., Slotow, R., Tenkanen, H., Moilanen, A., Heikinheimo, V., & Di Minin, E. (2018). Social media data can be used to understand tourists' preferences for nature-based experiences in protected areas. *Conservation Letters*, 11(1), 1–10.
<https://doi.org/10.1111/conl.12343>
- Houston, M. J., Bruskotter, J. T., & Fan, D. (2010). Attitudes toward wolves in the United States and Canada: A content analysis of the print news media, 1999–2008. *Human Dimensions of Wildlife*, 15(5), 389–403. <https://doi.org/10.1080/10871209.2010.507563>
- Hsieh, H.-F., & Shannon, S. E. (2005). Three approaches to qualitative content analysis. *Qualitative Health Research*, 15(9), 1277–1288.
<https://doi.org/10.1177/1049732305276687>
- Isaacs, J. C. (2000). The limited potential of ecotourism to contribute to wildlife conservation. *Wildlife Society Bulletin*, 28(1), 61–69. <https://doi.org/10.2307/4617284>

Kelling, S., Fink, D., La Sorte, F. A., Johnston, A., Bruns, N. E., & Hochachka, W. M. (2015).

Taking a 'Big Data' approach to data quality in a citizen science project. *Ambio*, 44, 601–611. <https://doi.org/10.1007/s13280-015-0710-4>

Kitchin, R. (2013). Big data and human geography: Opportunities, challenges, and risks.

Dialogues in Human Geography, 3(3), 262–267.

<https://doi.org/10.1177/2043820613513388>

Levin, N., Kark, S., & Crandall, D. (2015). Where have all the people gone? Enhancing global

conservation using night lights and social media. *Ecological Applications*, 25, 2153–2167. <https://doi.org/10.1890/15-0113.1>

Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., &

Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biological Conservation*, 215, 132–141. <https://doi.org/10.1016/j.biocon.2017.07.013>

Marsden, C., Woodroffe, R., Mills, M. G. L., McNutt, J. W., Creel, S., Groom, R., ... Mable, B.

K. (2012). Spatial and temporal patterns of neutral and adaptive genetic variation in the endangered African wild dog (*Lycaon pictus*). *Molecular Ecology*, 21(6), 1379–1393.

<https://doi.org/10.1111/j.1365-294X.2012.05477.x>

Müllner, A., Linsenmair, K. E., & Wikelski, M. (2004). Exposure to ecotourism reduces survival

and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, 118, 549–558. <https://doi.org/10.1016/j.biocon.2003.10.003>

Nghiem, L. T. P., Webb, E. L., & Carrasco, L. R. (2012). Saving Vietnam's wildlife through

social media. *Science*, 338(6104), 192–193.

<https://doi.org/10.1126/science.338.6104.192-b>

- Neuendorf, K. (2017). *The Content Analysis Guidebook*. Thousand Oaks, CA: SAGE Publications, Inc.
- Nortje, G. P., van Hoven, W., & Laker, M. C. (2012). Factors affecting the impact of off-road driving on soils in an area in the Kruger National Park, South Africa. *Environmental Management*, 50(6), 1164–1176. <https://doi.org/10.1007/s00267-012-9954-y>
- Person, D. K., & Russell, A. L. (2009). Reproduction and den site selection by wolves in a disturbed landscape. *Northwest Science*, 83(3), 211–224. <https://doi.org/10.3955/046.083.0305>
- Peterson, M. N., Birkhead, J. L., Leong, K., Peterson, M. J., & Peterson, T. R. (2010). Rearticulating the myth of human-wildlife conflict. *Conservation Letters*, 3(2), 74–82. <https://doi.org/10.1111/j.1755-263X.2010.00099.x>
- Range Wide Conservation Program for Cheetah & African Wild Dogs (RWCP). (2019). Range Wide Conservation Program for Cheetah & African Wild Dog. <http://www.cheetahandwilddog.org/>
- Rasmussen, G. (2009). *Anthropogenic factors influencing biological processes of the painted dog Lycaon pictus* [Doctoral dissertation, Oxford University]. Oxford University Research Archive. <https://libguides.bodleian.ox.ac.uk/digitaltheses/oxforddigitaltheses>
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D. W. (2008). Achilles heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. <https://doi.org/10.1086/590965>
- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286(3), 232–242. <https://doi.org/10.1111/j.1469-7998.2011.00874.x>

- Reynolds, P. C., & Braithwaite, D. (2001). Towards a conceptual framework for wildlife tourism. *Tourism Management*, 22(1), 31–42.
[https://doi.org/10.1016/s0261-5177\(00\)00018-2](https://doi.org/10.1016/s0261-5177(00)00018-2)
- Roffler, G. H., Gregovich, D. P., & Larson, K. R. (2018). Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat. *Forest Ecology and Management*, 409, 190–201. <https://doi.org/10.1016/j.foreco.2017.11.025>
- RWCP & IUCN/SSC. (2015). *Regional Conservation Strategy for the Cheetah and African Wild Dog in Southern Africa*; Revised and Updated, August 2015.
- Sidorovich, V., Schnitzler, A., Schnitzler, C., & Rotenko, I. (2017). Wolf denning behaviour in response to external disturbances and implications for pup survival. *Mammalian Biology*, 87, 89–92. <https://doi.org/10.1016/j.mambio.2016.11.011>
- Smith, D., Stahler, D., Cassidy, K., Stahler, E., Metz, M., Cassidy, B., ... Koitzsch, K. (2019). Yellowstone National Park Wolf Project Annual Report 2018. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2019-02.
- Stepchenkova, S., Kirilenko, A. P., & Morrison, A. M. (2009). Facilitating content analysis in tourism research. *Journal of Travel Research*, 47(4), 454–469.
<https://doi.org/10.1177/0047287508326509>
- Storch, I. (2013). Human disturbance of grouse—why and when? *Wildlife Biology*, 19(4), 390–403. <https://doi.org/10.2981/13-006>
- Thiel, R. P., Merrill, S., & Mech, L. D. (1998). Tolerance by denning wolves, *Canis lupus*, to human disturbance. *Canadian Field Naturalist*, 122(2), 340–342.
<http://www.npwrc.usgs.gov/resource/2000/wolftol/wolftol.htm>

- Toivonen, T., Heikinheimo, V., Fink., C., Hausmann, A., Hiippala, T., Järv, O., ... Di Minin, E. (2019). Social media data for conservation science: A methodological review. *Biological Conservation*, 233, 298–315. <https://doi.org/10.1016/j.biocon.2019.01.023>
- van der Wal, R., & Arts, K. (2015). Digital conservation: An introduction. *Ambio*, 44(4), S517–S521. <https://doi.org/10.1007/s13280-015-0701-5>
- Welz, A. (2017). Unnatural surveillance: how online data is putting species at risk. *Yale Environment 360*, 44(2), 135–147. Retrieved from <https://e360.yale.edu/features/unnatural-surveillance-how-online-data-is-putting-species-at-risk>
- Wood, S., Guerry, A. D., Silver, J. M., & Lacayo, M. (2013). Using social media to quantify nature-based tourism and recreation. *Scientific Reports*, 3(2976). <https://doi.org/10.1038/srep02976>
- Woodroffe, R., Davies-Mostert, H., Ginsberg, J., Graf, J., Leigh, K., McCreery, K., ... Szykman, M. (2007). Rates and causes of mortality in Endangered African wild dogs *Lycaon pictus*: Lessons for management and monitoring. *Oryx*, 41(2), 215–223. <https://doi.org/10.1017/s0030605307001809>
- World Tourism Organization. (2014). *Towards measuring the economic value of wildlife watching tourism in Africa: Briefing paper*. Madrid: World Tourism Organization.
- Wu, Y., Xie, L., Huang, S., Li, P., Yuan, Z., & Liu, W. (2018). Using social media to strengthen public awareness of wildlife conservation. *Ocean and Coastal Management*, 153, 76–83. <https://doi.org/10.1016/j.ocecoaman.2017.12.010>
- Zeng, B., & Gerritsen, R. (2014). What do we know about social media in tourism? A review. *Tourism Management Perspectives*, 10, 27–36. <https://doi.org/10.1016/j.tmp.2014.01.001>

Chapter III: Quantitative Photogrammetric Methodology for Measuring Mammalian Belly Score in a Large Carnivore

Abstract

The use of “belly-scoring” can offer a novel, noninvasive, objective management tool to accurately gauge food intake at individual, group, and population levels. Belly scores can also be used to monitor population fitness over time. As food availability is increasingly affected by predation, ecological competition, climate change, habitat modification and other human activities, an accurate belly scoring tool can facilitate comparisons among wildlife populations, thereby serving as an early warning indicator of threats to wildlife population health and potential population collapse. In social species, belly scores can also be an invaluable tool to understand social behavior and ranking. Here the first rigorous quantitative photogrammetric measurement methodology to measure belly scores of wild painted dogs (*Lycaon pictus*) was developed and applied. This methodology involves: (a) collating photographs of the lateral side of an individual at a right angle to the dorso/lateral profile, (b) photogrammetrically measuring belly chord length and “belly drop,” and (c) adjusting belly chord length as a departure from a standardized leg angle. This belly score method was applied to 631 suitable photographs of 15 painted dog packs that included 186 individuals, all collected between 2004–2015 from allopatric painted dog populations in and around Hwange and Mana Pools National Parks in Zimbabwe. Variation in mean belly scores exhibited a cyclical pattern throughout the year, corresponding to biologically significant patterns in prey availability. These results also highlighted significant differences between belly scores of the two different populations assessed, indicating potential food stress in the Hwange population. This standardized methodology provides a reliable management tool that can be applied to monitor the fitness of wild and captive individuals, social groups, and populations of painted dogs and other

endangered large carnivores in the face of growing direct and indirect anthropogenic disturbances that pose a threat to their survival.

Keywords: rapid assessment tool, population fitness, conservation, *Lycaon pictus*, painted dog, wildlife management, Zimbabwe, wildlife health, conservation biology

Introduction

Regular monitoring of animal populations is critical to facilitate detection of trends (e.g., reproductive success, number of individuals) within and between populations (Dauwalter & Rahel, 2009; Meyer et al., 2010). This can be done through traditional wildlife monitoring methods such as censuses, but these options are expensive, time consuming, and/or labor intensive (Gaidet-Drapier et al., 2006; Gonzalez et al., 2016). In conjunction with more traditional methods, rapid assessment tools such as body condition scoring may be more cost and time efficient, to date however, these tools are mostly subjective and have not been used to their full potential (DelGiudice et al., 2011; Zielke, Wrage-Mönnig, & Müller, 2018).

For example, beginning in 1988 the painted dog (*Lycaon pictus*) population in Kruger National Park, South Africa, was surveyed every five years using photographs of individual dogs collected by tourists (Maddock & Mills, 1994; Marnewick et al., 2014; Wilkinson, 1995). From 1988–1995, these 5-year surveys indicated a healthy population that fluctuated between ± 400 individuals. Between the 1995 and 2000 surveys however, an estimated 100 individuals were observed (Davies-Mostert et al., 2010). In the absence of more routine monitoring and rapid assessment tools, variation in rainfall was proposed as a potential factor for the steep population decline, but no direct cause was identified (Buettner et al., 2006; Mills, 1995). Here I propose a tool for rapidly assessing body condition that may assist with monitoring individuals and populations for early detection of health issues, both *in-situ* and *ex-situ*.

Body Condition Scoring

Body condition scoring is a management tool applied to both wild and domestic animals to measure, assess, and monitor the health of individuals and populations (Schiffmann et al., 2017). For wild animals, accurately measuring body condition generally involves the stress and cost of capture and restraint, which may inhibit the collection of meaningful sample sizes

(Boitani & Powell, 2012). Alternatively, monitoring body indices rather than body condition alone can prove to be more practical for assessing changes to the health of wildlife populations. Changes in body indices can arise as a response to changing ecological and anthropogenic conditions and may result from increased stress and reduced food intake, leading to a variation in reproductive success, and ultimately, declining populations (DeGiudice et al., 2011; Lane et al., 2014). A commonly applied method for large, free-ranging animals is to subjectively score body condition visually based on an ordinal scale (Fernando et al., 2009). This includes estimating the relative size or distension of an individual's stomach as a means of assessing fitness level with respect to how full the stomach is, i.e., relative hunger or satiation level (Knobel, du Toit, & Bingham, 2002; Woodroffe, Ginsberg, & Macdonald, 1997). These mostly subjective tools however have the disadvantage of being less rigorous for evaluating population trends, and are potentially subject to interobserver error and variation.

Terminology and methods vary for subjective visual measuring of body conditions (Giles et al., 2014). Examples of such terms include 'belly fullness score' (Knobel et al., 2002), 'belly size' (Packer, 1986), and 'belly score' (Bertram, 1975; Lehmann et al., 2008a, b; Woodroffe et al., 1997). These measurement methods were tested on large wild carnivores in the 1970s and 1980s, first on lions (*Panthera leo*; Bertram, 1975), whereby the stomach content volume or mass was visually estimated by viewing the profile of a standing lion. This visual estimation technique to assess food intake on a relative and subjective scale has since been applied to other lion studies (Lehmann et al., 2008a, b; Packer, 1986), as well as to cheetahs (*Acinonyx jubatus*; Caro, 1987; Frame & Frame, 1977) and painted dogs (Knobel et al., 2002). Caro (1987) found that mother cheetahs with larger litters had lower belly size (i.e., were thinner) and attributed this to the mother needing to spend more time hunting to feed her cubs. Knobel et al. (2002) reported

that belly fullness score was the same for all individuals in painted dog packs after hunting based on 22 trials that involved setting out bait for the animals. But without a reliable or standardized methodology, these results may not be meaningful.

One shortcoming of subjective visual estimation of belly size to gauge stomach contents is the use of variable scales with no reference to visually discrete morphometric points. These subjective visual estimation methods are prone to inconsistent estimates and observer bias, leading to associated criticism regarding reliability (Schiffmann et al., 2017; Woodroffe et al., 1997). The use of an algorithm approach (as offered here) provides a structured process for obtaining body scores from multiple structural regions of the body on individuals in photographs, introducing inherently less interobserver bias and variability (Schiffmann et al., 2017), particularly with the assistance of software measuring tools. For example, photogrammetric measurements were reliably used to measure painted dog cranial asymmetry (Edwards et al., 2013) and morphometric differences in painted dog populations across Africa (Shumba et al., 2017), as well as life stages of marbled salamanders (*Ambystoma opacum*; Mott et al., 2010). For this method, I define discrete morphometric points as anatomical points that are easily identified and distinguished by multiple observers, thereby minimizing observer and measurement bias.

Another challenge of subjective visual estimation of belly size and body condition is the lack of consistency in condition scaling across studies. Woodroffe et al. (1997) recommended that subjective belly scoring scales be limited to three to five categories and proposed a belly size scale of 1 to 4 (pp. 141–142). Bertram's (1975) original subjective belly score scale for wild lions ranged from 1 (fully distended) to 5 (empty); a scale designed to assess the stomach weight of animals that are able to consume large amounts of food in one feeding. Packer (1986) also applied a scale to wild lions ranging from 1 (fattest possible) to 5 (thinnest). Knobel et al.'s

(2002) belly fullness score for wild painted dogs ranged from 1 (empty) to 4 (belly markedly distended). For cheetahs, Caro (1987) applied a subjective visual assessment scale of 1 (near starvation) to 14 (a cheetah leaves a partially consumed kill), concluding that cheetahs typically begin to hunt at a belly scale of 5 or less.

Quantitative vs. Visual Estimation

In addition to the challenges mentioned, visual methods of estimating belly size use ordinal categorical scales that may mask subtle relationships within the data. Quantitative objective measurement on a continuous scale (i.e., measurements from a photograph determined objectively by software measuring tools) rather than subjective visual categorization offers a more accurate and repeatable method to monitor belly size (Schiffmann et al., 2017) as a means to score body condition and individual fitness. For large mammals such as carnivores, assessing body condition and fitness can be achieved relatively easily by taking photographs using a predetermined, standardized method and then accurately and objectively measuring relative body proportions and ratios of body proportions (Schiffman et al., 2017).

Accurate measurements of body condition relative to food consumption levels can also be obtained from photographs relative to measurement units (e.g., centimeters, meters) of objects if the dimensions of, or distance to, those objects are known (Shrader, Ferreira, & van Aarde, 2006). For example, photographs from overflying aircraft, including drones, at known altitudes and camera focal lengths have been used to measure body condition of free-ranging cetaceans (e.g., in meters), including gray whales (*Eschrichtius robustus*; Perryman & Lynn, 2002), right whales (*Eubalaena glacialis* and *E. australis*; Miller et al., 2012), and killer whales (*Orcinus orca*; Fearnbach et al., 2011). These measurements can then be equated to nutritional condition/fatness relative to changes in environmental conditions, food availability, and reproductive status. For free-ranging species in forested and remote environments, various

photographic methods have been successfully used to assess relative morphometric measurement and analysis. Examples include photographs of sedated wild animals with a reference of known scale (e.g., ruler) included in the photograph (Bertram, 1975), and relative assessments of body condition using remotely placed motion-sensor camera traps (Pérez-Flores, Calmé, & Reyna-Hurtado, 2016).

Example of Quantitative Belly Score Measurements

To date, only one study has attempted to objectively measure belly scores from lateral photographs in painted dogs (Potgieter & Davies-Mostert, 2012); however, discrete points, anatomy, or leg angles were not considered. In addition, this approach did not integrate the more refined measurement method as proposed here, nor did it describe how the measurements were derived (e.g., use of photogrammetric software and pixel count), a constraint making it difficult to repeat. The authors did conclude that more studies were needed to increase the sample size, including more tests of the approach among wild painted dogs.

The method proposed below is based on mammalian anatomy and focuses on the distance between the juncture of the floating ribs and those attached to the sternum (i.e., where belly distention starts), as well as the tangents to the lowest point of the belly as discrete measuring points. As a cursorial widely-ranging carnivore, individual painted dogs can maximally consume $\pm 40\%$ of their body weight in a short period of time (Rasmussen et al., 2008). This ability to quickly consume large amounts of meat is believed to be an evolutionary adaptation to maximize food consumption, easily carry food large distances to feed pups back at the den (Rasmussen et al., 2008), and minimize the risk of kleptoparasitism by lions and spotted hyenas (*Crocuta crocuta*; Carbone et al., 2005).

Here an objective and replicable methodology to systematically quantify relative belly scores based on recognizable discrete morphometric reference points is demonstrated. These

reference points are visible on photographs of painted dogs oriented perpendicular to the camera. Relative measurements for belly scores are based on the number of pixels from digital images using software measurement tools that produce standardizable and repeatable measurements, and subtended angles, from which trigonometrically-based corrections from the standard leg angle (here defined as 83°) can facilitate derivation of a relative belly score index.

Methods

Study Area

The primary study locations were Hwange National Park and Mana Pools National Park, and the areas surrounding each park in northern and western Zimbabwe (hereafter referred to as the Hwange and Mana Pools regions). Land bordering Hwange National Park includes public communal lands utilized for crop cultivation and livestock ranching, and private concessions that offer photographic and hunting safaris (Shumba et al., 2017). This semi-arid habitat has a mean seasonal rainfall of approximately 600 mm, which occurs primarily from November through March (the wet season; Dudley et al., 2003; Shumba et al., 2017). Daily temperatures generally range from 26°C to >40°C during the dry season, and average around 30°C during the wet season (Safari Bookings, 2019). The landscape is mainly woodland and scrubland, but also includes savanna and grasslands (Dudley et al., 2003). African teak (*Baikiaea plurijuga*), acacia (*Acacia spp.*), mopane (*Colophospermum mopane*), bush willows (*Combretum spp.*), and silver cluster-leaf (*Terminalia sericea*) are typical of the primary vegetation (Rasmussen, 1999). Known prey species of painted dogs in this region include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), and duiker (*Sylvicapra grimmia*; Rasmussen, 1999). Other large carnivores inhabiting the region include lions and spotted hyenas, both considered competitors and predators of painted dogs, as well as leopards (*Panthera pardus*; van der Meer et al., 2013).

Similar to Hwange National Park, Mana Pools National Park is adjacent to safari areas that offer photographic and hunting safaris and other recreational activities such as canoeing, fishing, and camping (Dunham & du Toit, 2012; Monks, 2008), although no hunting is allowed within the park itself (Monks, 2008). The Zambezi River comprises the northern boundary between Zambia and Zimbabwe, and mean rainfall is approximately 700 mm during the rainy season between November and April (Dunham & du Toit, 2012; Monks, 2008). In this region,

average daily temperatures range from 19°C in July to 29°C in October (Ndoro et al., 2016). Habitat varies from floodplain with mainly *Faidherbia albida* woodland along the Zambezi River to valley floor *Xylia torreana* dry forests, *Acacia tortillas* woodland savannah, and *Colophospermum mopane* woodlands (Monks, 2008). Primary painted dog prey species in this area include kudu, impala, eland (*Taurotragus oryx*), and smaller antelope species. Lions, leopards, and hyenas are also present (Zimbabwe Parks and Wildlife Management Authority [ZPWMA], 2017).

Focal Species

The Endangered (IUCN) painted dog is a highly social, cooperatively hunting species with large pack home ranges (Courchamp & Macdonald, 2001; Creel, 2001). Painted dogs are currently limited to isolated and severely reduced populations in sub-Saharan Africa, which persist despite historical campaigns to exterminate them as predatory vermin (Childes, 1988; Edwards et al., 2013; Fanshawe, Frame, & Ginsberg, 1991; Marsden et al., 2012). Remaining populations are primarily scattered across national parks and managed game parks in South Africa, Tanzania, Kenya, Zimbabwe, Zambia, Namibia, Botswana, and Mozambique (Fanshawe et al., 1991; RWCP, 2019). Many remaining populations are not considered viable, and as documented in Cameroon, countrywide extirpations occur (Croes et al., 2012).

Painted dog populations, and those of many other species, are increasingly vulnerable to direct (e.g., bushmeat poaching, vehicular accidents) and indirect (e.g., habitat destruction, food availability, climate change) impacts of human activity. These many threats urgently require effective solutions, including the development of promising rapid assessment tools. As highlighted by the Kruger example, the ability to rapidly monitor the health of remnant painted dog populations is essential for the quick detection of changes within and between populations. Systematic and quantitative monitoring of belly scores is therefore a valuable and practical tool

to track the viability of local populations. For instance, a painted dog pack consisting of 8 to 10 adults and yearlings is considered the most efficient, under optimal conditions, at maximizing prey consumption and reproduction relative to their energetic requirements (Courchamp, Rasmussen, & Macdonald, 2002; Rasmussen et al., 2008). Information collected via this belly score method could be used to examine the health and social dynamics associated with equal food sharing and partitioning among pack members (Rasmussen et al., 2008), or to illustrate differences with other large carnivores that have more hierarchical systems such as lions (Packer, 1986), wolves (*Canis lupus*; Mech, 1999), and spotted hyenas (Tilson & Hamilton III, 1984).

Data Collection

Photographs of painted dogs were collected continuously from 2004–2015 during a long-term behavioral ecology study of the species in the Hwange and Mana Pools regions. Camera-trap images (Stealth Cam model STC-G42NG, STC-G45NG) and photos from three HD digital Nikon Coolpix cameras were obtained from the Painted Dog Research Trust (PDRT) staff. Images from safari operators and tourists were also solicited and obtained. To avoid pseudoreplication, duplicate images of the same dog at the same time event (e.g., within the same hour) were not used. Data collected included date, time, location (latitude and longitude), group size and composition (e.g., adult, subadult, pup), individual painted dog ID, image number, and photographer/source contact information. Suitable images were defined as those taken of either the right or left lateral side of each painted dog at a right angle (i.e., perpendicular), with the axilla, front leg angle, belly, and sacroiliac process all visible.

Image Processing

Three morphometric measurements based on discrete, easily recognizable morphometric points (Figures 3-1 and 3-2) were selected to calculate belly scores; dorsal tip of scapula to lateral epicondyle in the front leg (FL), belly chord length (BCL), and belly drop (BD; Figures

3-1 and 3-2; definitions in Table 3-1). Adobe Photoshop's measurement tool was used to obtain these three measurements in pixels for all suitable images. This measurement tool was chosen because it allows users to identify, and zoom in on, discrete points, thereby minimizing measuring error. In addition to recording the pixels for each of the three measurements above, the vertical chord angle (VC) and horizontal chord angle (HC; definitions in Table 3-1) were documented for each image. These two angle values are also automatically displayed by Adobe when obtaining the FL and BCL measurements, and are used to facilitate finding the angle between the FL and BCL, denoted as Θ .

Here I explain why the VC and HC angles were recorded in addition to the pixel measurements. Using a standardized morphometric photograph that exhibited "good posture" (individual standing with all four feet touching the ground; Figure 3-1), I used the 83° leg angle (Θ) as the standard. The deviation from the standard leg angle (Θ minus 83) was denoted as Δ (Table 3-2). Depending on whether Θ was greater or less than 83 , the formula to correct the BCL was: Adjusted BCL = $BCL \pm FL * \tan \Delta$ (Table 3-2). The Adjusted BCL was used to develop a standardized belly score across different postures (i.e., leg angles).

Data were entered into an Excel spreadsheet (see example in Table 3-3), with the associated formulas provided in Table 3-2.

Interrater Reliability

To test interrater reliability, an intraclass correlation coefficient (ICC; two-way random effects model, absolute agreement, for single observations where both users and measurements were treated as random effects) was calculated using IBM SPSS version 26, $\alpha = 0.05$. Koo and Yi (2016) stated that there is a lack of acceptable reliability standards for ICC, but noted that at least 30 samples and 3 raters should be used when possible. The corresponding ICC value scale

for such a sample is: poor reliability if values are less than 0.5, moderate reliability for values between 0.5 and 0.75, good reliability for values between 0.75 and 0.90, and excellent reliability if values are greater than 0.90 (Koo & Yi, 2016). For this study, five users were given a tutorial and then asked to record the FL, BCL, and BD measurements, and corresponding VC and HC angles (Figure 3-1; definitions in Table 3-1), for 10 preselected photos of painted dogs. To reduce measuring error, users maximally “zoomed in” to the discrete morphometric points and drew reference lines before measuring. Although our sample size was smaller than that suggested by Koo and Yi (2016), we used the proposed value scale to assess our results.

Table 3-1

Definitions of morphometric terms used to calculate relative belly score for Lycaon pictus

Term	Abbreviation	Definition
Front Leg	FL	Measurement with a line that begins at the highest point of scapula (shoulder blade) and extends to the lateral epicondyle on the elbow
Vertical Chord Angle	VC	Angle of leg obtained when measuring FL from dorsal to ventral points
Belly Cord Length	BCL	Measurement with a line that begins with the protrusion of the sacroiliac process (below the tail) and extends to the axilla (front armpit), following the edge of the floating ribs
Horizontal Chord Angle	HC	Angle of leg obtained when measuring BCL from posterior point (sacroiliac process) to anterior point (armpit)
Belly Drop	BD	Measurement with a line that extends from the discrete point juncture between the sternum-attached and floating ribs to the distal bottom profile of the belly

Table 3-2

Formulas used in Excel spreadsheet to derive belly scores for Lycaon pictus from morphometric measurements

Calculation	Formula
Leg angle Θ	Absolute value (HC – VC)
Angular adjustment (degrees) Δ	Leg angle - 83
Angular adjustment (radians)	Radians (Leg angle - 83)
BCL adjustment (pixels)	Tangent (Angular adjustment radians)*BCL
Adjusted BCL	BCL + BCL adjustment (pixels)
Belly score	Belly drop / Adjusted BCL

Table 3-3

Example of Excel spreadsheet for morphometric measurement data entry. Formulas to calculate belly scores for Lycaon pictus from these measurements are pre-entered into the appropriate cells

File Name	FL	VC	BCL	HC	Leg angle	Angular adjustment (degrees)	Angular adjustment (radians)	BCL adjustment (pixels)	Adjusted BCL	Belly drop	Belly score
Standardized image, 83° leg angle	335.06	81.10	593.16	164.10	83.00	0.00	0.00	0.00	593.16	90.97	0.1533
Front leg forward (BCL increases)	335.06	83.10	614.80	164.10	81.00	-2.00	-0.03	-21.47	593.33	90.97	0.1533
Front leg backward (BCL decreases)	335.06	79.10	573.13	164.10	85.00	2.00	0.03	20.01	593.14	90.97	0.1533

Figure 3-1

Example of suitable photograph of painted dog (Lycaon pictus) showing front leg (FL), belly chord length (BCL) and belly depth (BD) measurements and leg angle (denoted by Θ) used to obtain belly score. Image courtesy of Greg Rasmussen.

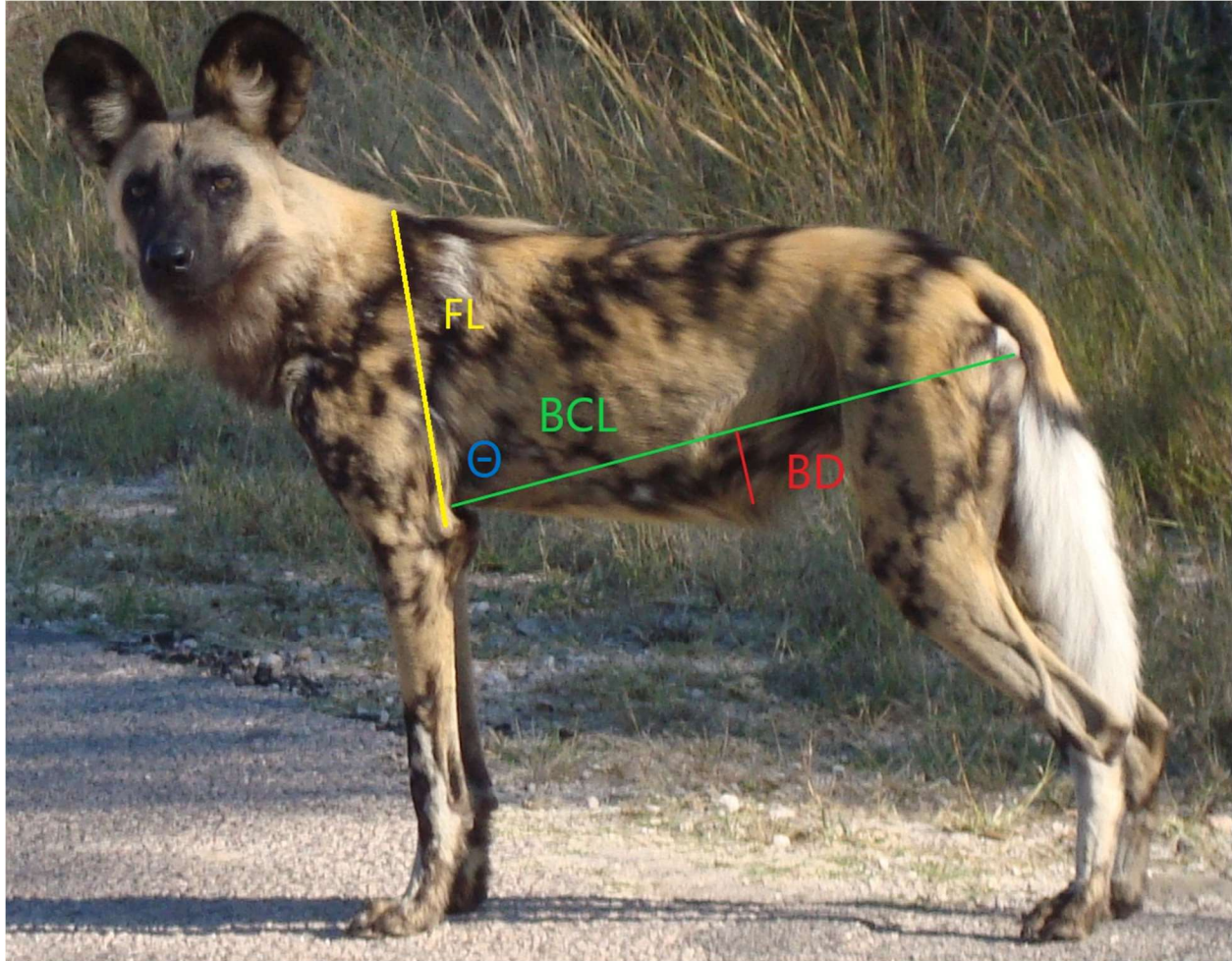
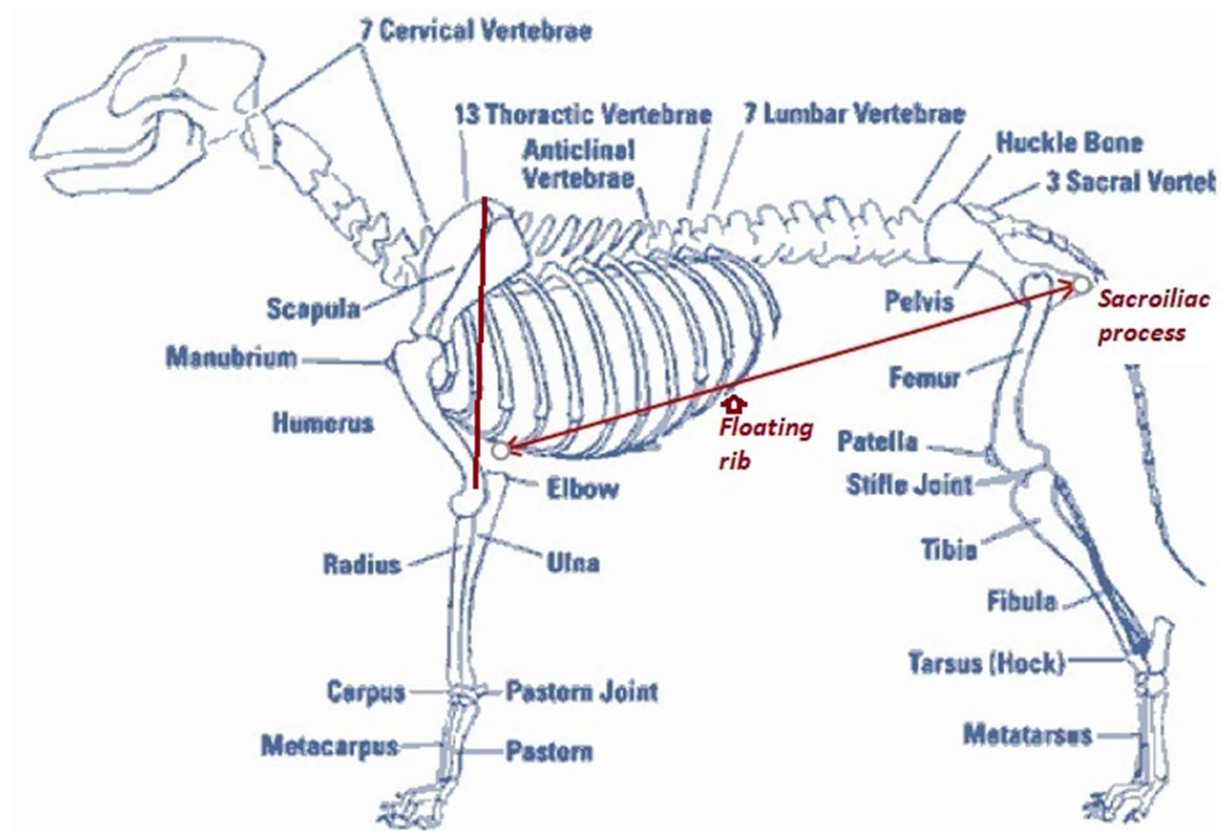


Figure 3-2

African painted dog (Lycaon pictus) skeletal structure demonstrating floating ribs and discrete points from which morphometric measurements to calculate belly score were derived. Image courtesy of Greg Rasmussen.



Data Analysis

Belly scores calculated for all suitable images were normally distributed based on the visual assessment of a distribution plot using SPSS. Mixed effects models were run in SPSS to test whether calculated belly scores (the response variable) were related to predictor variables (e.g., region [Hwange or Mana Pool] and month). As some individual dogs were present in multiple images, individual dogs were included as a random effect. Region (Hwange or Mana Pools) and month were both treated as fixed effects. A t-test revealed there was no effect of sex

(i.e., no difference in belly scores between males and females), and therefore, sex was not included in these models.

Results

ICC was 0.927 (95%, CI = 0.840 – 0.966), corresponding to “good” to “excellent” reliability (i.e., > 0.75 and 0.90, respectively) on the ICC value scale. The average difference across all users and all three measurements (i.e., FL, BCL, and BD) was 0.18%, and individual differences ranged from 0 to 1.59%.

A total of 631 photographs of 186 individual dogs from 15 packs were analyzed. Belly scores ranged from 0.121 to 0.143 between the two regions (Table 3-3). There was a significant difference in mean belly scores between the Hwange and Mana Pools populations ($F_{1,118.0}=10.721$, $p=0.001$), as well as significant variation in mean belly scores among months for both populations ($F_{1,139.4}=8.596$, $p=0.004$).

Mean belly scores peaked in April/May and November for individuals in both the Hwange and Mana Pools regions with smaller peaks in January for both populations (Figure 3-3). Both populations exhibited similar seasonal variations, and there was no significant interaction between seasonal variation and region ($F=0.629$, $df=11.59$, $p=0.804$). The lowest belly score (corresponding to less stomach distension, which presumably represents reduced food intake and/or high pup demand) occurred during the month of July in Mana Pools; other cyclical lows for that area were evident during March (Figure 3-3).

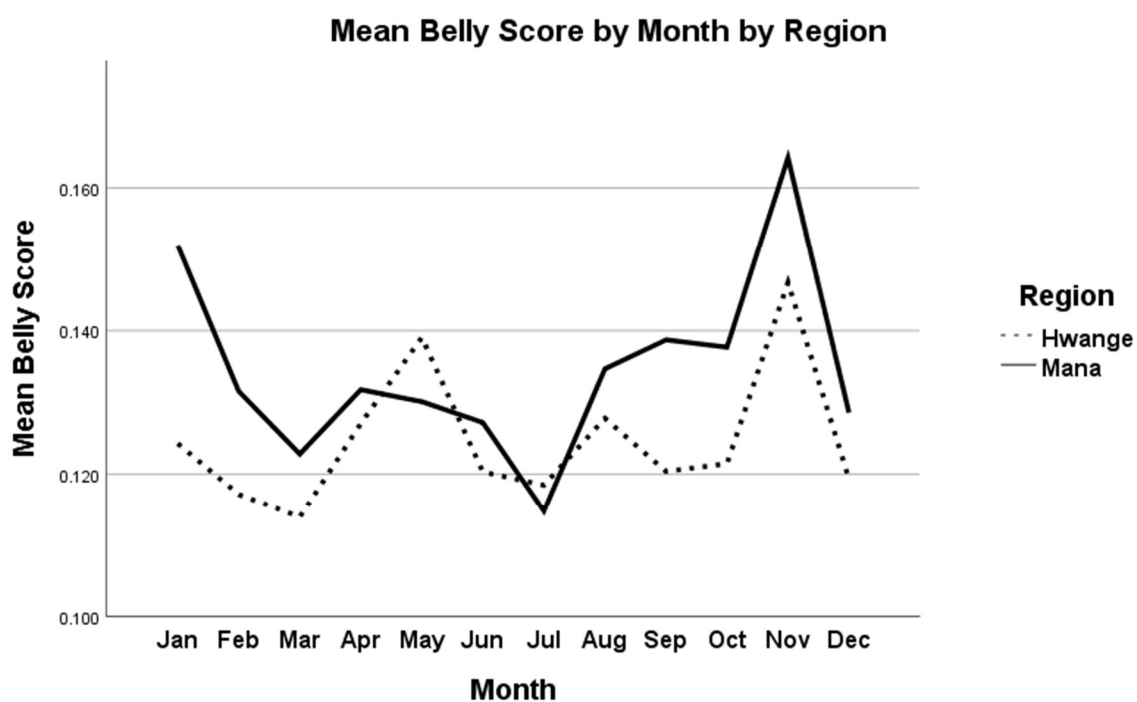
Table 3-4

Summary statistics of Lycaon pictus belly score means in Hwange and Mana Pool regions from suitable photographs obtained from 2004–2015

Belly score	Mana Pools Region	Hwange Region
Mean	0.138	0.126
Standard error	0.003	0.002
Minimum/Maximum	0.132/0.143	0.121/0.130

Figure 3-3

Monthly variation in Lycaon pictus belly score means between the Hwange and Mana Pools regions, Zimbabwe



Discussion

Subjectivity is decreased with this systematic belly score approach that relies on specific and easily identifiable morphometric measuring points, allowing for more accurate comparisons among individuals and populations. Furthermore, although these measurements facilitate physical comparisons, they can also yield ecologically relevant information such as the similar seasonal patterns exhibited by both populations. Previous use of belly scores among wild species has been limited to ordinal-scaled or subjective visual appraisals. Although these may offer quick assessments, they lack discrete morphometric reference points and do not account for leg position or angle. This may introduce ‘noise’ in the data and mask finer scaled relationships, but can also present problems with respect to accuracy and precision, as well as challenges to replicating the approach in other studies.

The cyclical pattern in mean belly scores demonstrated by both populations throughout the year corresponds to biologically meaningful patterns; increased belly scores during both prey rutting and lambing/calving seasons, and food stress during the painted dogs’ denning season. For example, the mean belly score was highest during November, the peak lambing season for impala and peak calving season for kudu (primary prey species of painted dogs; Rasmussen, 1999). In contrast, mean belly scores were lower in May and July, corresponding with the regional denning season for painted dogs and a presumed reduced food intake for individuals due to regurgitating for pups (Courchamp et al., 2002). This is consistent with Giles et al.’s (2014) claim that seasonal variation in body condition is an evolutionary adaptation to survive stochastic, seasonal environments.

Gestation and lactation are energetically costly to many species (Miller et al., 2012), but particularly to painted dogs (Rasmussen et al., 2008). Disturbance of any kind while raising pups may exacerbate these costs. One plausible explanation for the lower belly scores in Hwange

relative to Mana Pools is that given high baseline reproduction costs, further food stress as a result of habitat modifications via elephants and/or human activity (Cumming, 1982) may impose additional energetic costs, potentially leading to differences in body indexes.

Furthermore, the intentional alteration or creation of infrastructure designed to attract wildlife for human viewing and profit may have unanticipated impacts on painted dogs and their prey. One such scenario involves the creation of artificial waterholes in the Hwange region that attract elephants and other wildlife (Valeix et al., 2009). With these modifications, wildlife may deviate from their otherwise natural roaming behavior to remain nearer where resources are plentiful. In the case of elephants, their population numbers can increase (Cumming, 1982), exceeding the natural carrying capacity. In Hwange, this higher relative density has resulted in decreased vegetation and an altered ecosystem structure, which in turn leads to a decrease in both prey availability and suitable denning habitat for painted dogs (Rasmussen, 2009; Valeix et al., 2009).

Management Implications

These findings indicate that belly scores can serve as an important management tool for monitoring free-ranging populations of painted dogs, as well as potentially having practical applications to other carnivore species of concern. Uses can include comparisons among individuals, packs (e.g., pack size), age groups (i.e., pup, yearling, adult), and sex, between or among seasons and years. This method can assist with assessing general body conditions of individuals and populations relative to prey availability, habitat disturbance, human activity (Chapter II), presence or abundance of interspecific competitors, and current wildlife management practices for both short studies and long-term monitoring efforts. This can also be extremely useful in facilitating comparisons in population health among painted dog populations in different regions, and indeed, for carnivores in general.

The seasonal variation in belly scores for these two populations show how belly scores may provide an overview of the health and status of painted dog populations in particular, and ecosystems in general. For example, declining belly scores in painted dogs during denning season were demonstrated, indicating painted dogs are already stressed during this sensitive and critical period. If additional stressors negatively affect prey availability or increase competition by intraguild predators (i.e., lions and hyenas), increased energetic costs can result in decreased reproductive success, litter size, and pup survival for painted dogs. Using belly scores to routinely monitor painted dogs and other species can offer early indicators of additional stressors such as a decrease in prey species, allowing for intervention or further investigation. In addition, incorporating both belly scores and climate data may allow patterns to emerge that indicate how painted dogs and other species may be impacted by climate change.

Captive wildlife managers may benefit from this methodology as well. Although many captive animals are trained to perform behaviors that allow health assessments (e.g., offering a paw for blood draws, stepping on scales to obtain body mass) while the animal is awake, other animals must be sedated. Obtaining belly scores from images can allow zoological facilities to noninvasively monitor some animals without use of sedation. In addition, this information can be shared among caretakers, allowing for comparisons among individual animals and institutions. Belly scores can also be used with standardized morphometric measurements (Chapter V) to provide additional information relating to life stages, diet, growth, and development.

In the face of declining and disappearing wildlife populations, rapid noninvasive assessment tools such as body condition scoring can also offer conservation biologists and protected area managers low-cost monitoring options that are easily replicated. When performed in the context of citizen science, such as through the evaluation of tourist photos (Marnewick et

al., 2014), these tools may yield relatively robust data. This study used over 600 images collected during an 11-year behavioral ecology study. A more concentrated effort that incorporates camera traps, tourists, researchers, zoo staff and visitors, social media (Chapter II), and other sources could yield a suitable sample size in a much shorter time frame. Additionally, involving the public not only assists with data collection that may guide management decisions, but also provides an opportunity to educate them about pressing conservation and environmental issues (Shumba et al., 2017). Although public inclusion may require additional resources such as time, staff, and funding, rapid assessment tools such as this can facilitate increased data collection and allow more information to be more efficiently and rapidly analyzed, and the results shared.

References

- Bertram, B. C. R. (1975). Weights and measures of lions. *East African Wild Life Society*, 13, 141–143. <https://doi.org/10.1111/j.1365-2028.1975.tb00128.x>
- Boitani, L., & Powell, R. A. (Eds.). (2012). *Carnivore Ecology and Conservation: A Handbook Of Techniques*. New York, NY: Oxford University Press.
<https://doi.org/10.1644/13-MAMM-R-122.1>
- Buettner, U. K., Davies-Mostert, H. T., du Toit, J., & Mills, M. G. L. (2006). Factors affecting juvenile survival in African wild dogs (*Lycaon pictus*) in Kruger National Park, South Africa. *Journal of Zoology*, 272, 10–19.
<https://doi.org/10.1111/j.1469-7998.2006.00240.x>
- Carbone, C., Frame, L., Frame, G., Malcolm, J., Fanshawe, J., FitzGibbon, C., ... du Toit, J. T. (2005). Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology*, 266(2), 153–161.
<https://doi.org/10.1017/S9052836905006710>
- Caro, T. M. (1987). Cheetah mothers' vigilance: looking out for prey or for predators? *Behavioral Ecology and Sociobiology*, 20, 351–361. <https://doi.org/10.1007/BF00300681>
- Childes, S. L. (1988). The past history, present status and distribution of the hunting dog *Lycaon pictus* in Zimbabwe. *Biological Conservation*, 44, 301–316.
[https://doi.org/10.1016/0006-3207\(88\)90022-5](https://doi.org/10.1016/0006-3207(88)90022-5)
- Courchamp, F., & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog (*Lycaon pictus*). *Animal Conservation*, 4, 169–174.
<https://doi.org/10.1017/S1367943001001196>

- Courchamp, F., Rasmussen, G. S. A., & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13(1), 20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15, 271–274. <https://doi.org/10.1111/j.1523-1739.2001.99534.x>
- Croes, B., Rasmussen, G., Buij, R., & de Longh, H. (2012). Status of the African wild dog in the Benoue Complex, North Cameroon. *Canid News*. Retrieved from http://www.canids.org/canidnews/15/African_wild_dogs_in_Cameroon.pdf
- Cumming, D. H. M. (1982). The influence of large herbivores on savanna structure in Africa. In B. J. Huntley & B.H. Walker (Eds.), *Ecology of Tropical Savannas* (pp. 217–245). vol 42. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-68786-0_11
- Davies-Mostert, H. T., Burger, M., Mills, M. G. L., Somers, M., Hofmeyr, M., & Ferreira, S. (2010). *Baseline results of the 5th wild dog and 3rd cheetah photographic census of Greater Kruger National Park*. South African National Parks. https://www.sanparks.org/parks/kruger/conservation/scientific/noticeboard/science_network_meeting_2010/Presentations/Davies-MostertHT.pdf
- Dauwalter, D. C., & Rahel, F. J. (2009). Temporal variation in trout populations: Implications for monitoring and trend detection. *Transactions of the American Fisheries Society*, 138, 38–51. <https://doi.org/10.1577/T07-154.1>
- DelGiudice, G. D., Sampson, B. A., Lenarz, M. S., Schrage, M. W., & Edwards, A. J. (2011). Winter body condition of moose (*Alces alces*) in a declining population in northeastern Minnesota. *Journal of Wildlife Diseases*, 47(1), 30–40.

<https://doi.org/10.7589/0090-3558-47.1.30>

- Dudley, J. P., Criag, G. C., Gibson, D. ST. C., Haynes, G., & Klimowicz, J. (2003). Drought mortality of bush elephants in Hwange National Park. *African Journal of Ecology*, 39, 187–194. <https://doi.org/10.1046/j.0141-6707.2000.00297.x>
- Dunham, K. M., & du Toit, A. J. (2012). Using citizen-based survey data to determine densities of large mammals: a case study from Mana Pools National Park, Zimbabwe. *African Journal of Ecology*, 51, 431–440. <https://doi.org/10.1111/aje.12052>
- Edwards C. T. T., Rasmussen. G. S. A., Riordan P., Courchamp F., & Macdonald D. W. (2013). Non-adaptive phenotypic evolution of the endangered carnivore *Lycaon pictus*. *PloS ONE*, 8(9). <https://doi.org/10.1371/journal.pone.0073856>
- Fanshawe, J. H., Frame, L. H., & Ginsberg, J. R. (1991). The wild dog—Africa's vanishing carnivore. *Oryx*, 25(3), 137–146. <https://doi.org/10.1017/S0030605300034165>
- Fearnbach, H., Durban, J. W., Ellifrit, D. K., & Balcomb III, K. C. (2011). Size and long-term growth trends of endangered fish-eating killer whales. *Endangered Species Research*, 13, 173–180. <https://doi.org/10.3354/esr00330>
- Fernando, P., Janaka, H. K., Ekanayaka, S. K. K., Nishantha, H. G., & Pastorini, J. (2009). A simple method for assessing elephant body condition. *Gajah*, 31, 29–31. <https://doi.org/10.5167/uzh-32262>
- Frame, G. W., & Frame, L. H. (1977). Serengeti cheetah. *Wildlife News*, 12(3), 2–6.
- Gaidet-Drapier, N., Fritz, H., Bourgarel, M., Renaud, P-C., Poilecot, P., Chardonnet, P., ... Le Bel, S. (2006). Cost and efficiency of large mammal census techniques: comparison of methods for a participatory approach in a communal area, Zimbabwe. *Biodiversity and Conservation*, 15, 735–754. <https://doi.org/10.1007/s10531-004-1063-7>

- Giles, S. L., Nicol, C. J., Harris, P. A., & Rands, S. A. (2014). Dominance rank is associated with body condition in outdoor-living domestic horses (*Equus caballus*). *Applied Animal Behaviour Science*, 166, 71–79. <https://doi.org/10.1016%2Fj.applanim.2015.02.019>
- Gonzalez, L. F., Montes, G. A., Puig, E., Johnson, S., Mengersen, K., & Gaston, K. J. (2016). Unmanned aerial vehicles (UAVs) and artificial intelligence revolutionizing wildlife monitoring and conservation. *Sensors*, 16(1), 97, <https://doi.org/10.3390/s16010097>
- Knobel, D. L., du Toit, J. T., & Bingham, J. (2002). Development of a bait and baiting system for delivery of oral rabies vaccine to free-ranging African wild dogs (*Lycaon pictus*). *Journal of Wildlife Diseases*, 38(2), 352–362. <https://doi.org/10.7589/0090-3558-38.2.352>
- Koo, T. K., & Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of Chiropractic Medicine*, 15(2), 155–163. <https://doi.org/10.1016/j.jcm.2016.02.012>
- Lane, E. P., Clauss, M., Kock, N. D., Graham Hill, F. W., Majok, A. A., Kotze, A., & Codron, D. (2014). Body condition and ruminal morphology responses of free-ranging impala (*Aepyceros melampus*) to changes in diet. *European Journal of Wildlife Research*, 60, 599–612. <https://doi.org/10.1007/s10344-014-0824-1>
- Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *South African Journal of Wildlife Research*, 38(1), 66–78. <https://doi.org/10.3957/0379-4369-38.1.66>
- Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, 43(2), 230–236. <https://doi.org/10.3377/1562-7020-43.2.230>

- Maddock, A. H., & Mills, M. G. L. (1994). Population characteristics of African wild dogs *Lycaon pictus* in the Eastern Transvaal Lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67(1), 57–62.
[https://doi.org/10.1016/0006-3207\(94\)90009-4](https://doi.org/10.1016/0006-3207(94)90009-4)
- Marnewick, K., Ferreira, S. M., Grange, S., Watermeyer, J., Maputla, N., & Davies-Mostert, H. T. (2014). Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PloS ONE*, 9(1), e86265. <https://doi.org/10.1371/journal.pone.0086265>
- Marsden, C.D., Woodroffe, R., Mills, M. G. L., McNutt, J. W., Creel, S., Groom, R., ... Mable, B. K. (2012). Spatial and temporal patterns of neutral and adaptive genetic variation in the endangered African wild dog (*Lycaon pictus*). *Molecular Ecology*, 21(6), 1379–1393.
<https://doi.org/10.1111/j.1365-294X.2012.05477.x>
- Mech, L. D. (1999). Alpha status, dominance, and division of labor in wolf packs. *USGS Northern Prairie Wildlife Research Center*, 381, 1196–1203.
<http://digitalcommons.unl.edu/usgsnpwrc/381>
- Meyer, C. F. J., Aguiar, L. M. S., Aguirre, L. F., Baumgarten, J., Clarke, F. M., Cosson, J-F., ... Kalko, E. K. V. (2010). Long-term monitoring of tropical bats for anthropogenic impact assessment: Gauging the statistical power to detect population change. *Biological Conservation*, 143, 2797–2807. <https://doi.org/10.1016/j.biocon.2010.01.029>
- Miller, C. A., Best, P. B., Perryman, W. L., Baumgartner, M. F., & Moore, M. J. (2012). Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. *Marine Ecology Progress Series*, 459, 135–156. <https://doi.org/10.3354/meps09675>

- Mills, M. G. L. (1995). Notes on wild dog *Lycaon pictus* and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, 38(1): 95–99. Pretoria.
<https://doi.org/10.4102/koedoe.v38i1.309>
- Monks, N. J. (2008). *The demography and population status of lions (Panthera leo) in the Mana Pools National Park, Zimbabwe*. (Philosophiae Doctor), University of the Free State, Bloemfontein.
- Mott, C. L., Albert, S. E., Steffen, M. A., & Uzzardo, J. M. (2010). Assessment of digital image analyses for use in wildlife research. *Wildlife Biology*, 16(1), 93–100.
<https://doi.org/10.2981/09-010>
- Ndoro, O., Mashapa, C., Kativu, S., & Gandiwa, E. (2016). Impact of African elephant on baobab along a surface water availability gradient in Mana Pools National Park, Zimbabwe. *Tropical Ecology*, 57(2), 333–341.
- Packer, C. (1986). The ecology of sociality in felids. In D. I. Rubenstein and R. W. Wrangham (Eds.), *Ecological Aspects of Social Evolution: Birds and Mammals* (pp. 429–452). Princeton, NJ: Princeton University Press.
- Pérez-Flores, J., Calmé, S., & Reyna-Hurtado (2016). Scoring body condition in wild Baird's tapir (*Tapirus bairdii*) using camera traps and opportunistic photographic material. *Tropical Conservation Science*, 9. <https://doi.org/10.1177/1940082916676128>
- Perryman, W. L., & Lynn, M. S. (2002). Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *Journal of Cetacean Research and Management*, 4(2), 155–164.

- Potgieter, K. R., & Davies-Mostert, H. T. (2012). A simple visual estimation of food consumption in carnivores. *PloS ONE*, 7(5), e34543.
<https://doi.org/10.1371/journal.pone.0034543>
- Range Wide Conservation Program for Cheetah & African Wild Dogs (RWCP). (2019). *Range Wide*. Retrieved from <http://www.cheetahandwilddog.org/>
- Rasmussen, G. (1999). Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation*, 99, 133–139.
[https://doi.org/10.1016/S0006-3207\(98\)00006-8](https://doi.org/10.1016/S0006-3207(98)00006-8)
- Rasmussen, G. (2009). *Anthropogenic factors influencing biological processes in the painted Dog Lycaon pictus* (Unpublished doctoral dissertation). University of Oxford, United Kingdom.
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D. W. (2008). Achilles heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. <https://www.jstor.org/stable/10.1086/590965>
- Safari Bookings (Hwange NP). (2019). *Weather & Climate – Hwange NP*. Retrieved from <https://www.safaribookings.com/hwange/climate>
- Schiffmann, C., Clauss, M., Hoby, S., & Hatt, J-M. (2017). Visual body condition scoring in zoo animals—composite, algorithm and overview approaches in captive Asian and African elephants. *Journal of Zoo and Aquarium Research*, 5, 1–10.
<https://doi.org/10.19227/jzar.v5i1.252>
- Shrader, A. M., Ferreira, S. M., & van Aarde, R. J. (2006). Digital photogrammetry and laser rangefinder techniques to measure African elephants. *South African Journal of Wildlife Research*, 36(1), 1–7. <https://hdl.handle.net/10520/EJC117233>

- Shumba, T., Montgomery, R. A., Rasmussen, G. S. A., & Macdonald, D. W. (2017). African Wild dog habitat use modelling using telemetry data and citizen scientist sightings: are the results comparable? *African Journal of Wildlife Research*, 48(1).
<https://doi.org/10.3957/056.048.013002>
- Tilson, R. L., & Hamilton III, W. J. (1984). Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour*, 32(3), 715–724.
[https://doi.org/10.1016/S0003-3472\(84\)80147-5](https://doi.org/10.1016/S0003-3472(84)80147-5)
- Valeix, M., Loveridge, A. J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23–30.
<https://doi.org/10.1890/08-0606.1>
- van der Meer, E., Rasmussen, G. S. A., Muvengwi, J., & Fritz, H. (2013). Foraging costs, hunting success and its implications for African wild dog (*Lycaon pictus*) conservation inside and outside a protected area. *African Journal of Ecology*, 52(1), 69–76.
<https://doi.org/10.1111/aje.12092>
- Wilkinson, I. (1995). *The 1994/1995 wild dog photographic survey*. South African National Parks unpublished report, South African National Parks, Skukuza.
- Woodroffe, R., Ginsberg, J. R., & Macdonald, D. W. and the IUCN/SSC Canid Specialist Group. 1997. *The African Wild Dog – Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland. 166 pp.
- Zielke, L., Wrage-Mönnig, N., & Müller, J. (2018). Development and assessment of a body condition score scheme for European bison (*Bison bonasus*). *Animals*, 8(163).
<https://doi.org/10.3390/ani8100163>

Zimbabwe Parks and Wildlife Management Authority (ZPWMA). (2017). Mana Pools.

Retrieved from <http://zimparks.org/parks/national-parks/mana-pools/>

Chapter IV: Do Human-Created Trails Influence the Presence of African Carnivores and Herbivores?

Abstract

Wildlife related tourism generates positive opportunities for communities and conservation, but also leads to negative direct and indirect costs to wildlife and the environment. This includes impacts on the activities (e.g., foraging) of wildlife, habitat degradation, and increased mortality. Some species use hiking, biking, and/or motor vehicle trails created by humans to travel or hunt. Here the potential of human-modified game trails to influence the presence of mammalian carnivore and herbivore species was investigated in the Hwange-Matetsi Complex in Zimbabwe; an area frequented by tourists to view wildlife, hunt game, and participate in other recreational activities. Existing game trails were widened (labeled as “modified”) and compared with subsequent mammal activity on game trails not altered by humans (labeled as “unmodified”). This was done by quantifying the usage of modified and unmodified trails by five carnivore species and seven herbivore species, evaluating latent time to first detection for carnivores and herbivores on each trail type, and noting time of day of carnivore and herbivore presence via data collected on camera traps. These data also provided the opportunity to characterize the mammalian community in the study area. It was anticipated that carnivores would be observed more frequently on modified trails, whereas herbivores would be recorded primarily on unmodified trails; carnivores would be observed on modified trails sooner than unmodified trails, and that carnivore and herbivore activity periods would differ from each other and between trail type. Thirty-one different mammal species were detected in the study area. Results showed that the five carnivore species were observed on modified trails more frequently than unmodified trails, whereas six of the seven herbivore species were recorded on unmodified trails more frequently; though no species used one type of trail significantly more than another. Latent time

to first observation for both carnivores and herbivores was not significantly different for either group or trail type. However, the time of day (i.e., morning, midday, evening) that carnivores and herbivores was active was significantly different. Although these findings suggest that the issue of human modifications at a fine scale would benefit from further investigations, they are not inconsistent with the expectation that carnivores would use human-modified trails more frequently than herbivores. Additional research, including samples from a greater diversity of study sites, should be collected in similar contexts to better understand how tourism activities might facilitate changes to animal activity and movements, and the implications that such changes might have for effective policies and management plans involving protected areas, tourism, wildlife, and the intersection of these sectors.

Keywords: recreation ecology, wildlife viewing, recreational trails, off-road activity, human disturbance, anthropogenic impacts, Zimbabwe

Introduction

Often perceived as less harmful than consumptive activities (e.g., hunting, fishing), non-consumptive activities such as wildlife viewing can lead to direct and indirect threats to wildlife (Müllner, Linsenmair, & Wikelski, 2004; Storch, 2013; Wolf, Croft, & Green, 2019). Human presence, through tourism and other recreational activities, can negatively impact species fitness by affecting diel activity (Corcoran et al., 2013; Ladle, Steenweg, Shepherd, & Boyce, 2018), foraging behavior (Dunn, Hamer, & Benton, 2010), immune responses (French, DeNardo, Greives, Strand, & Demas, 2010), body mass of young individuals (Almasi, Beziers, Roulin, & Jenni, 2015), and population recruitment (Broekhuis, 2018). These effects may be short or long-term (Marion, Leung, Eagleston, & Burroughs, 2016; Scholten, Moe, & Hegland, 2018) and can vary in intensity depending on whether human activities are, among other factors, motorized or nonmotorized (Ladle et al., 2018; Olson, Squires, Roberts, Ivan, & Hebblewhite, 2018; Spaul & Heath, 2016) or conducted on- or off-road (Heinmeyer et al., 2019; Nortje, van Hoven, & Laker, 2012; Wolf & Croft, 2010). Because wildlife-related tourism ranks as a top attraction worldwide (World Tourism Organization, 2014), these impacts can potentially lead to regional or global population changes, an important consideration for threatened and endangered species.

One concern among conservation professionals and scientists is that benefits associated with wildlife-related tourism (e.g., revenue, community participation and empowerment) may be overshadowed by their potentially negative impacts on wildlife (Higginbottom, Northrope, & Green, 2001; Kruger, 2005). The field of recreation ecology (Marion et al., 2016; Monz, Pickering, & Hadwen, 2013), or the study of how outdoor activities and associated “influential factors” (Marion et al., 2016, p. 352) impact the environment, is helping to shed light on these relationships. One particular area of recreation ecology was investigated in this study: how trails

created or modified by humans affect the occurrence or detection of mammalian carnivore and herbivore species. This is particularly important given that many tourists expect to have close encounters with nature when participating in activities such as wildlife viewing (Reynolds & Braithwaite, 2001). This expectation can incentivize tour guides and operators to engage in actions that are potentially harmful to wildlife, including driving off-road, regardless of the impacts these activities might have on wildlife or the ecosystem (Macdonald et al., 2017; Nortje et al., 2012; Reynolds & Braithwaite, 2001). Whereas some impacts may be direct (e.g., change in wildlife behavior) and immediately observable (e.g., multiple vehicles surrounding an animal; Macdonald et al., 2017), others may be indirect (e.g., wildlife avoiding areas with human activity) or “invisible,” and therefore relatively unknown.

The initial establishment of a trail creates soil compaction, leading to cascading effects in an ecosystem (Marzano & Dandy, 2012; Nortje et al., 2012). These effects include directly affecting the presence and movement of various species. Heinmeyer et al. (2019) noted that wolverines (*Gulo gulo*) avoided areas where both motorized and nonmotorized activities occurred. They further observed that female wolverines were more sensitive to these disturbances (Heinmeyer et al., 2019). Wolf and Croft (2010) investigated the responses of kangaroo species to foot and vehicular traffic, as well as on- versus off-road approaches. They found that individuals in general, and females in particular, exhibited stronger negative responses to off-trail activities. Species other than mammals are also affected by recreational activities: Spaul and Heath (2016) observed that golden eagle (*Aquila chrysaetos*) reproductive success was negatively associated with off-road vehicle and pedestrian activity.

Another important consideration relating to recreational trail creation and use is the potential for human activity to influence the movement and/or behavior of species to exploit new

areas and resources. This can be particularly worrisome when such activities facilitate predation of or competition with threatened and endangered species, whose reproductive success and fitness may decrease as a result. One such endangered carnivore, the African painted dog (*Lycaon pictus*), is a popular species for viewing among tourists (Gusset et al., 2008; Lindsey, Alexander, du Toit, & Mills, 2005). Painted dogs typically den in woodland habitat (Creel & Creel, 2002; van der Meer et al., 2013), so in some cases, tour guides must leave primary roads to locate and drive to den sites. Here an emerging concern and theory is introduced, one that could negatively impact painted dog survival and is in need of further scrutiny: wildlife tourism groups may inadvertently lead or facilitate the movement of larger carnivores (i.e., lions [*Panthera leo*] and spotted hyenas [*Crocuta crocuta*]) to painted dog dens by creating trails from primary roads to den sites, endangering both painted dog adults and pups. Thus, this study was conducted during the months when painted dogs typically den. Painted dogs were believed to be denning within the study site; however, the location or number of dens was not confirmed.

The goal for this study was to determine which carnivore and herbivore species in the Hwange-Matetsi Complex in Zimbabwe were more likely to use or avoid human-modified trails. To investigate how human-modified trails influence the presence of carnivore and herbivore species, existing game trails (i.e., trails created and used by wildlife) were cleared and/or expanded to simulate trails used by humans (referred to as “modified” trails), and camera-traps were used to compare the presence of different mammal species on them with unaltered game trails (referred to as “unmodified” trails) while characterizing the mammalian community with by-catch data (Welch, Grant, & Parker, 2019). Carnivore and herbivore usage of modified and unmodified trails, average number of days before carnivores and herbivores were observed on each trail type, and time of day carnivores and herbivores were observed using each trail type

were evaluated. It was expected that carnivores would be observed more frequently on modified trails, whereas herbivores would show a preference for unmodified trails.

Methods

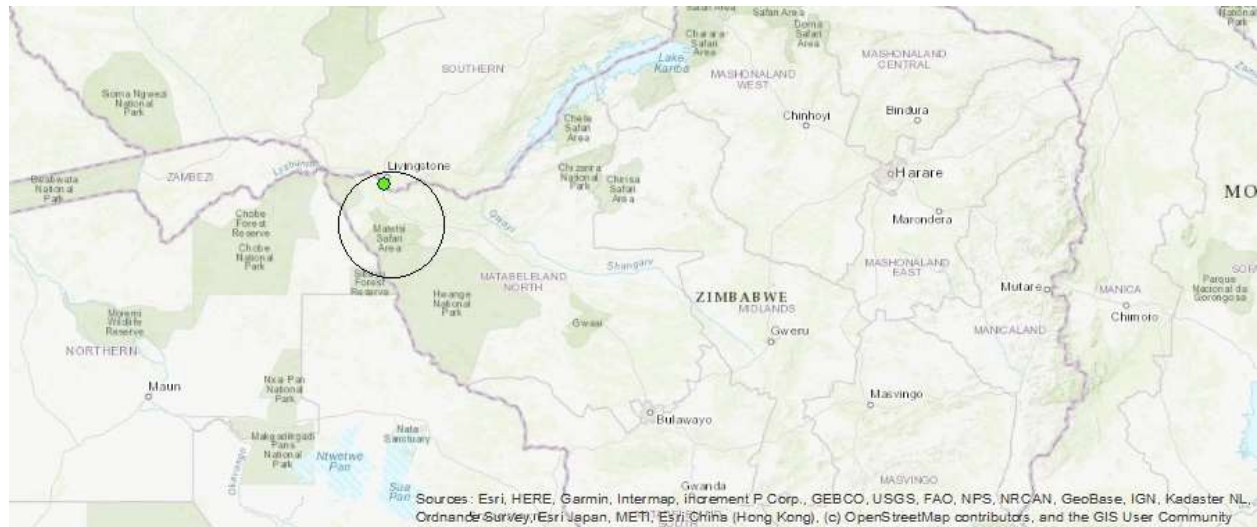
Study Area

The Hwange-Matetsi Complex in northwestern Zimbabwe encompasses approximately 90,000 hectares (ZPWMA, 2017a) and includes Matetsi Safari Area, Zambezi National Park, Deka Safari Area, and Kazuma Pan National Park (Figure 4-1). Tourism is the third largest industry in Zimbabwe after mining and agriculture (Steinmetz, 2017), and tourism activities within the study site include camping, hunting, fishing, photography, wildlife viewing, and boat cruises (ZPWMA, 2017a, b).

Mean annual rainfall is approximately 600 mm, most of which occurs between November and March (the wet season; Dudley, Criag, Gibson, Haynes, & Klimowicz, 2001; Shumba, Montgomery, Sillero-Zubiri, & Rasmussen, 2017). Daily temperatures can range from 26°C to over 40°C during the dry season, and average around 30°C during the wet season (Safari Bookings, 2019). The landscape consists mainly of semi-arid, subtropical woodland and scrubland, but also includes savanna and grasslands (Dudley et al., 2001). African teak (*Baikiaea plurijuga*), acacia (*Acacia spp.*), mopane (*Colophospermum mopane*), bush willows (*Combretum spp.*), and silver cluster-leaf (*Terminalia sericea*) are among the primary vegetation species (Rasmussen, 1999). Carnivores known to inhabit this region include lions, spotted hyena, African painted dogs, and leopards (*Panthera pardus*; Shumba et al., 2017; van der Meer, Mpofu, Rasmussen, & Fritz, 2013). Herbivores found in this region include African elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), sable antelope (*Hippotragus niger*), and common duiker (*Sylvicapra grimmia*; Mhlanga, Ramesh, Kalle, Madiri, & Downs, 2018; Rasmussen, 1999).

Figure 4-1

Hwange-Matetsi Complex study site in northwestern Zimbabwe (general location highlighted by circle). Green circle indicates Victoria Falls. Image courtesy of Misty Libby.



Identification of Potential Modified and Unmodified Trail Sites

A preliminary assessment for the potential placement of study trails was conducted by driving primary roads to identify the presence (as indicated by tracks, fecal droppings, or physical sightings) of two large carnivores: lions and spotted hyenas. Upon confirming recent carnivore activity, existing game trails that could be further cleared and/or widened were identified. Existing game trails were necessary as “modified” trails were superimposed on them or left unaltered so they could be used as controls. Once a potential site was identified where a trail could be modified, one camera trap (Stealth Cam model STC-G42NG or STC-G45NG) was placed perpendicular to the primary road at the beginning of that potential study trail. All camera traps were securely fastened to trees approximately 70–80 cm off the ground where they operated for approximately 1–2 weeks to determine carnivore presence prior to trail modification. If no carnivores were recorded during that time, that trail was not selected for inclusion in the study.

Modified and Unmodified Trails

Five of the trails where carnivore presence was detected on the primary road were modified starting from where the camera trap was originally placed along the primary road. Trails that contained ‘curves’ or ‘bends’ were intentionally chosen so they had less straight-line visibility. These trails were then widened and cleared of vegetation using a handheld grass slasher, branches, and the research team’s feet and until they were approximately 30–50 m long and 1–2 m wide (Figure 4-2). A second camera trap was then placed perpendicular to the trail at the “end” of the cleared portion of the trail.

To serve as “controls” for comparison purposes, an equal number of trails were left unaltered (Figure 4-3). These unmodified trails were generally within 200–600 m of a modified trail and contained the same camera trap sampling scheme. However, these unmodified trails were not explicitly paired with adjacent or nearby modified trails. Although no modifications were made to the control trails themselves, it is recognized that the installation of camera traps constituted some level of modification.

In an effort to expand data collection within the study site beyond the 10 trails (five modified, five unmodified) with a paired camera trap setup, 15 additional trails were monitored via single camera traps. Rather than having one camera trap along the primary road, and one on the trail, the additional set of eight modified trails and seven unmodified trails each contained one camera trap set at the intersection of the primary road and beginning of the trail. For the overall study, 35 camera traps were placed on 25 trails: 13 modified trails (five with two camera traps, eight with one camera trap), and 12 unmodified or “control” trails (five with two camera traps, seven with one camera trap). Camera traps operated in the field 24 hrs/day for between 30–150 days from June–November 2018. All camera trap locations were recorded via a handheld GPS device. Rechargeable batteries were replaced every 1–2 weeks, and images from each

camera SD card were downloaded during battery changes to minimize researcher presence in the area and in the event of damage to the units. During the course of the study, three cameras and all of their accompanying data were lost (one damaged by a hyena, one damaged by a bush fire, one SD card failure of unknown origin); they were therefore removed from further analysis. In addition, due to some trails only having one camera trap along the primary road, only data from camera traps that were located along the primary road were used for data analysis.

Figure 4-2

Modified trail (i.e., existing game trail that was cleared and/or widened). Image courtesy of author.



Figure 4-3

Unmodified trail (i.e., existing game trail that was unaltered and used as a control). Image courtesy of author.



Data Processing

All images on all SD cards from each camera were reviewed and all images where no animals were present were deleted. If an animal was present in an image, the species, date, and time the image was taken was recorded, as well as the temperature and camera location. If an animal was present but unidentifiable, the species was labeled as “unknown.” Because of the diversity of species observed, representative carnivores and herbivores known to inhabit the study area (Mhlanga et al., 2018; Shumba et al., 2017; van der Meer et al., 2013) were chosen for analysis. Carnivores consisted of one meso-carnivore, the side-striped jackal (*Canis adustus*), and four large carnivores: African lion, spotted hyena, painted dog, and leopard. Seven herbivores ranging in size from small to very large based on Miller, Pitman, Mann, Fuller, and Balme’s (2018) size categories were selected. Small (<25 kg) and medium (<100 kg) herbivores included the common duiker and impala, respectively. Kudu and sable antelope were labeled as large herbivores (<350 kg), and African buffalo, African elephant, and giraffe (*Giraffa spp.*) were categorized as very large (>350 kg) herbivores.

Images were considered independent if they occurred at least 15 minutes apart. Although common intervals for independence used in previous camera trap studies are 30 minutes to one hour (Davis, Kelly, & Stauffer, 2011; Merson, Dollar, Tan, & Macdonald, 2019; Rovero & Zimmermann, 2016), 15 minutes was deemed appropriate in this case because the interest was related to species usage of trails rather than simply species abundance or occupancy. The number of independent images of each species observed for each camera, as well as across all cameras for all trails, was summarized. Because camera deployment varied from 30 days to 150 days, capture effort was standardized by dividing the number of animals observed on each camera, and the total number of images of each species recorded on each camera, by the total number of nights each camera was deployed at a location.

Data Analysis

Carnivore and Herbivore Trail Usage

The total number of independent images of each species was calculated for each camera, and this value was divided by the number of nights a camera was deployed. For each of the two taxonomic groups (i.e., carnivores and herbivores), t-tests were used to evaluate differences in the number of images/camera trap night between modified and unmodified trails, where each camera served as a distinct sampling unit. In addition, as a separate analysis following Dillon and Kelly (2007), images were pooled from all modified and unmodified cameras and a X^2 contingency table analysis was conducted to evaluate whether the relative number of independent carnivore and herbivore images were associated with modified versus unmodified trails across all cameras of that type.

Latent Time to First Detection

The average number of days until an individual carnivore or herbivore was first observed on camera on a modified or unmodified trail was calculated by summing the number of days preceding first observations of individuals of both groups and dividing this value by the number of cameras that recorded these species or taxonomic groups. T-tests were done separately for both carnivore and herbivore groups, as well as for modified and unmodified cameras but did not include camera traps where individuals from either group were not observed.

Time of Day Species Observed

Three categories were created for time of day based on the general disparity between the crepuscular or nocturnal activity patterns of carnivores such as hyenas, lions (Mugerwa, du Preez, Tallents, Loveridge, & Macdonald, 2017), and painted dogs (Rasmussen, Gusset, Courchamp, & Macdonald, 2008), and the timing of most game drives for wildlife viewing (i.e., dawn and dusk): “AM” = 6:00 am–12:00 pm, “MID” = 12:01 pm–6:00 pm, and “PM” = 6:01

pm–5:59 am. The number of each species observed for each time period was summarized across all cameras, and a X^2 goodness-of-fit test was used to evaluate whether the relative number of independent carnivore and herbivore images was associated with different times of day across all camera traps.

Characterization of Mammalian Community

Individual animals that were identifiable to species were noted in a spreadsheet per the image sorting and processing protocol. Species occurrences across all cameras were summarized and tested for differences in richness of species (number of species present; Cusack et al., 2015; Welch et al., 2019) on modified and unmodified trails using t-tests, again with each camera trap serving as an independent sampling unit. All statistical analyses were conducted in R using $\alpha=0.05$.

Results

Carnivore and Herbivore Trail Usage

All five representative carnivore species were recorded on both modified and unmodified trails. Although all carnivores were observed on modified trails somewhat more frequently than unmodified trails, the difference was not significant ($t=-1.09$, $df=16.63$, $p=0.28$). Six of the seven herbivore species also utilized both types of trails. Herbivore species were observed on unmodified trails more frequently than modified trails, although also not significantly so ($t=0.59$, $df=12.40$, $p=0.57$). A chi-square test of independence showed that there was no significant association between species and trail type ($X^2=1.99$, $df=1$, $p=0.1578$).

Latent Time to First Detection

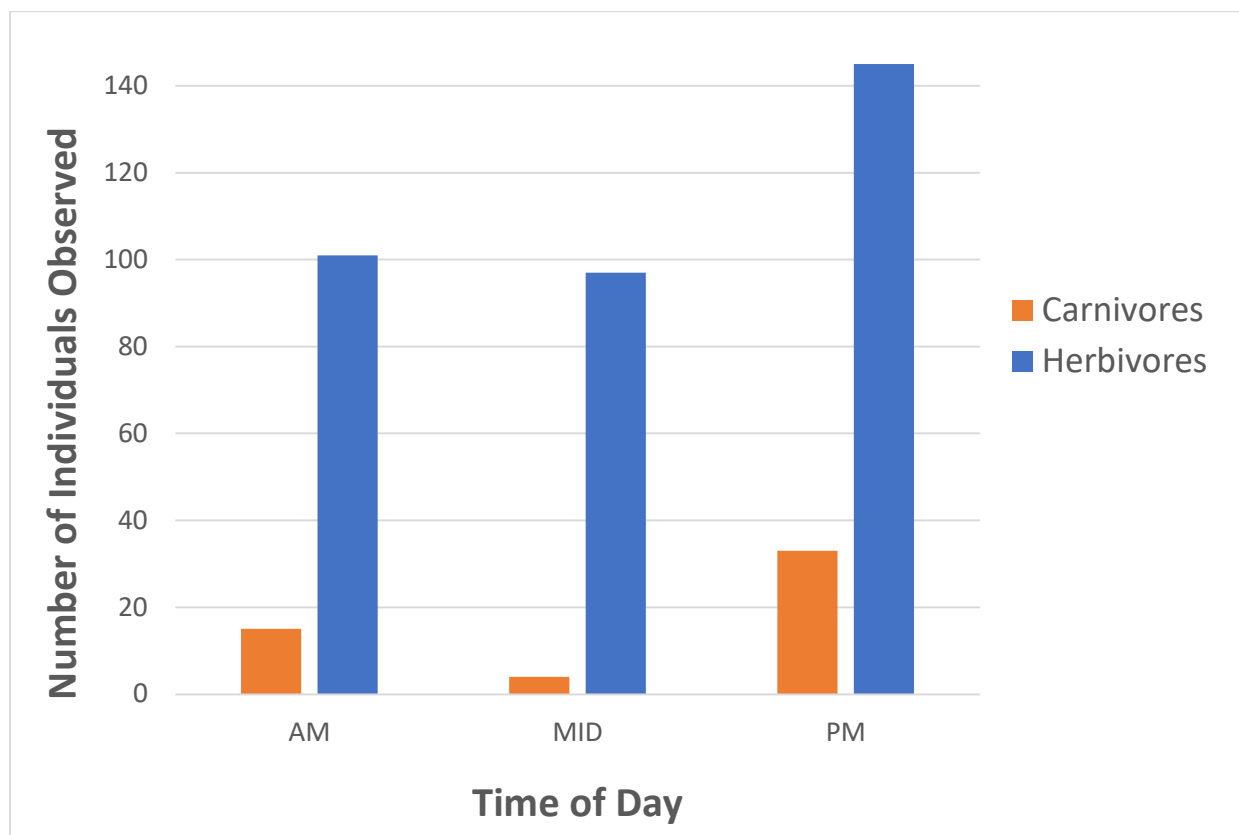
No significant difference was observed in how soon both carnivores and herbivores were recorded on modified trails (six days for carnivores, 8 days for herbivores) compared to unmodified trails (17 days for carnivores, 13 days for herbivores; $t=2.19$, $df=5.20$, $p=0.08$; $t=0.86$, $df=26.21$, $p=0.39$; carnivores and herbivores respectively).

Time of Day Species Observed

Time of day that carnivores and herbivores were observed was significantly different ($X^2=16.28$, $df=2$, $p=0.0003$). Carnivores were primarily observed in the PM (6:01 pm–5:59 am) category. Herbivores were observed in all three categories, with similar observation levels occurring in the AM and MID categories and increased observations in the PM (Figure 4-4).

Figure 4-4

Summary of time of day¹ carnivores and herbivores were observed using trails



¹Time of day categories: AM (6:00 am–12:00 pm), MID (12:01 pm–5:59 pm), PM (6:00 pm–5:59 am)

Characterization of Mammalian Community

A total of 31 identifiable (inclusive of the representative five carnivores and seven herbivores) species (Table 4-1) were observed in 544 images collected over 2,996 trap nights (unmodified=1342, modified=1654). Forty-two images contained species that could not be identified. Of the 31 species photographed, 29 were observed on modified trails and 22 were observed on unmodified trails (Table 4-1). The number of species recorded per camera trap ranged from 1–13, whereas the number of records of all species per camera ranged from 1–68. There was no significant difference in species richness ($t=-0.29$, $df=21.99$, $p=0.77$) on modified versus unmodified trails.

Table 4-1

All mammalian and avian species identified on camera traps on modified and unmodified trails from 32 sites collected over 2,996 trap nights

Common Name	Scientific Name	Number of Individuals Observed on Modified Trail	Number of Individuals Observed on Unmodified Trail
African lion	<i>Panthera leo</i>	4	1
African wild dog	<i>Lycaon pictus</i>	2	2
Spotted hyena	<i>Crocuta crocuta</i>	13	11
Leopard	<i>Panthera pardus</i>	3	1
Side-striped jackal	<i>Canis adustus</i>	5	1
African elephant	<i>Loxodonta africana</i>	54	57
Giraffe	<i>Giraffa spp.</i>	10	7
African buffalo	<i>Syncerus caffer</i>	5	3
Impala	<i>Aepyceros melampus</i>	0	3
Kudu	<i>Tragelaphus strepsiceros</i>	20	14
Sable antelope	<i>Hippotragus niger</i>	2	2
Duiker	<i>Sylvicapra grimmia</i>	40	25
Korhaan	<i>Eupodotis spp.</i>	3	4
Springhare	<i>Pedetes capensis</i>	2	0
African wild cat	<i>Felis silvestris</i>	11	1
Olive baboon	<i>Papio anubis</i>	40	23
Southern ground-hornbill	<i>Bucorvus leadbeateri</i>	7	4
African civet	<i>Civettictis civetta</i>	4	0
Honey badger	<i>Mellivora capensis</i>	5	1
Vervet monkey	<i>Cercopithecus pygerythrus</i>	2	2
Guinea fowl	<i>Numida meleagris</i>	0	2
Warthog	<i>Phacochoerus africanus</i>	6	4
Serval	<i>Felis serval</i>	1	0
Black-bellied bustard	<i>Lissotis melanogaster</i>	1	0
Bat-eared fox	<i>Otocyon megalotis</i>	1	0
Genet	<i>Genetta spp.</i>	1	1
Aardvark	<i>Orycteropus afer</i>	2	0
Smith's red rock rabbit	<i>Pronolagus spp.</i>	1	0
Slender mongoose	<i>Herpestes sanguinea</i>	1	0
Zebra	<i>Equus spp.</i>	1	0

Discussion

Despite the mix of significant and not statistically significant results, these findings were not inconsistent with original expectations and offer a foundation for further recreation ecology and wildlife management research for this region. To my knowledge, this is the first investigation of how species usage of, and diversity on, human-modified game trails contrast with species diversity and use of existing, unmodified game trails. The presence and/or abundance of specific carnivore and herbivore species on human-modified trails should be further evaluated via additional studies. Studies should also include smaller terrestrial vertebrates and the avian community such as has been done by Mugerwa, Sheil, Ssekiranda, van Heist, and Ezumea (2013) in Uganda as the initial creation of trails has an immediate impact on the local environment, with potentially cascading consequences at the ecosystem and landscape levels. In addition, prior studies in this study area have largely focused on individual species such as spotted hyenas (Mhlanga et al., 2018). Although Mhlanga et al. (2018) captured an average of 10 herbivore species across three sites in northwest Zimbabwe over 3600 camera trap days, findings consistent with species expected to be found in the region (Loveridge et al., 2017), this study's report of 31 bird and mammal species provides the first general overview of the terrestrial vertebrate community for the study area. Several species, including the serval (*Felis serval*), bat-eared fox (*Otocyon megalotis*), and rabbit (*Pronolagus spp.*), were detected only once.

That differences in the frequency and diversity of species using modified and modified trails was not significantly different may have been due to several factors, including, but not limited to the following: (a) low sample sizes, as evidenced by the low number of records for certain species; (b) the location/direction of the trail with respect to its purpose or direction humans or animals were traveling; and (c) ease of use or accessibility. Although trail location/direction and ease of use/accessibility by wildlife and humans is beyond the control of

researchers, low sample size can be remedied through the inclusion of additional trails and cameras that encompass a larger area or longer periods of time. The number of cameras per trail is an important consideration as well. Even though the majority of trails in this study had two cameras (one at the intersection of the trailhead and primary road and one at the end of the trail), some were left with one functioning camera due to damage or data loss. For data analysis consistency, only cameras that were located along the primary road were used. This of course excluded some data, which may also have affected sample size and results.

Future studies should also consider other elements of study design and sampling method (Cusack et al., 2015; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Kolowski & Forrester, 2017). One possibility is comparing “pre” and “post” modification images. This would entail setting cameras and collecting data on unmodified trails, then modifying half the trails and continuing to collect data to assess the differences “before” and “after.” Also, despite placing camera traps along primary roads used by humans and on game trails created and used by wildlife, the full extent of usage of both types of trails by various species may not have been captured. As Cusack et al. (2015) observed, species such as caracals (*Caracal caracal*) and African wild dogs that occur at low densities were only detected on trail-based cameras during the wet season in Tanzania. This may be the result of microhabitat preference, individual/species behaviors (i.e., following versus crossing trails), conspecific/competitor presence, physical size, or multiple other factors (Harmsen et al., 2010) such as trail width preference. Harmsen et al. (2010) documented an increased capture rate of jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*) on wide versus narrow trails.

It was expected that the five representative carnivores would be observed on modified trails, and while these species were seen using modified trails sooner than herbivores, herbivores

also appeared on modified trails sooner than unmodified trails. This may be due to herbivore species being more visible as they followed or crossed trails or the number of herbivore species and individuals present in the area, among other factors. In addition, some species could have triggered, but not been captured by, the camera traps, while others that used both modified and unmodified trails may have increased the likelihood of being photographed.

The time of day carnivores and herbivores used each type of trail was evaluated to investigate if observations of these two groups coincided with times of tourism activity. Differences in times species from each group were observed was determined to be statistically significant. Carnivores were observed on trails primarily in the PM category, with the majority of images captured during darkness or early AM (prior to 7:00 am). Mid-day (MID) sightings were lowest. This was not unexpected as carnivores typically hunt during the AM and PM timeframes, providing potential overlap between their foraging activities and human activities such as hunting and game drives (which typically take place around dawn and dusk). If humans are following existing roads or driving off-road, this may have unintended consequences such as interrupting foraging (e.g., scaring prey species or carcass abandonment) or conspecific interactions (van der Ree, Smith, & Grilo, 2015). While still damaging and disruptive, it has been suggested that driving vehicles on existing roads may be less disruptive than off-road activities (Scholten et al., 2018; Wolf & Croft, 2010). Herbivores were also observed more frequently in the PM time period, coinciding with carnivore foraging periods (Mugerwa et al., 2017), although herbivore observation levels were similar for both the AM and MID periods.

Regardless of the time of day of activity, for animals that rely on chemical signals such as odor plumes to navigate in search of prey or mates (Vickers, 2000), creating new trails opens up paths for odors to travel; allowing previously undetected den sites or prey to become detectable.

This may introduce another threat if new trails are created that lead to sensitive areas such as endangered species denning habitats. One example is the African wild dog, also called the painted dog. This species generally dens in woodland habitat that provides protection from large carnivores such as lions and spotted hyenas, cover for hunting, and protection from the elements (Creel & Creel, 2002; van der Meer et al., 2013). Should tour operators drive off-road towards a den, the trail may attract the curiosity of other species, including lions and spotted hyenas that have been known to injure or kill adult and young wild dogs (Creel & Creel, 2002).

Even if a trail does not lead directly to a sensitive area such as a den, opening a trail alters the habitat, leading to a cascade of consequences that are not fully understood. Such consequences may include carnivores such as lions and hyenas following or investigating human-modified trails, causing herbivores to avoid trails if carnivores were previously present on them. The inverse could be true as well. If herbivores use a trail that leads to a den, carnivores may be more apt to follow that same trail, particularly if the animal is a prey species. This can affect prey availability and predator abundance. In the case of African wild dogs, less prey and more competitors can lead to detrimental impacts. If wild dogs incur additional energetic costs to obtain prey that is scarce to feed adults and pups, and face increased competition and threat of injury or death from lions and hyenas, this can decrease the wild dog's reproductive success, health, fitness, and survival. In addition, decreased availability of primary prey may force wild dogs to switch prey items, again, with cascading consequences at multiple levels for both the wild dogs and biodiversity within that system.

Despite the negative impacts of humans creating trails, recreational ecology studies may offer positive opportunities. One example is the potential to monitor wildlife health. The noninvasive body condition assessment tool discussed in Chapter III can be used to assess and

compare the health of various species observed within and between study sites. If camera traps are set perpendicular to trails, suitable images (i.e., lateral view of each animal) of wildlife can be captured. Although the methodology in Chapter III is specific to wild dogs, standardized anatomical reference points can be pre-selected for species of interest, with camera heights adjusted accordingly. Tourists can also contribute to data collection through the sharing of observations made while participating in recreational activities as was done for painted dogs in Kruger National Park, South Africa (Maddock & Mills, 1994; Marnewick et al., 2014; Wilkinson, 1995).

Evaluating the effects of anthropogenic impacts on wildlife is a multi-faceted, interdisciplinary endeavor. Here I looked at two general groups of wildlife within a relatively small area to investigate possible consequences of human trail creation and use to wildlife. French et al. (2017) noted that it is important to quantify both the presence and extent of tourist activities, including those that are on- and off-road. Previous studies focused on observing the responses of birds (Müllner et al., 2004), fish (Bessa, Geffroy, & Goncalves-De-Freitas, 2017), reptiles (French et al., 2010), and marine mammals (Christiansen, Lusseau, Stensland, & Berggren, 2010) to the approach or presence of tourists in boats, vehicles, and on foot. Effects included altered activity patterns, habitat shifts, and decreased social behaviors (Bessa et al., 2017; Christiansen et al., 2010; Müllner et al., 2004; Storch, 2013); all of which may affect both carnivores and herbivores, particularly during critical life stages such as raising young (Rasmussen & Macdonald, 2012; Scholten et al., 2018).

It is acknowledged that although attempts were made to minimize the small-scale habitat alteration for this study through the clearing/expanding of existing game trails, species other than those observed may have been impacted. This, and the considerations discussed earlier, highlight

the need for further recreation ecology research and the impacts on individual animals, populations, or ecosystems. Recommendations include sampling a wider geographical area, sampling for longer periods (i.e., more camera trap nights), sampling across wet and dry seasons as was done by Mhlanga et al. (2018), and sampling both protected areas such as national parks as well as private land. As wildlife related tourism is a popular global activity, and habitat alteration is one of many consequences of this activity, there can be broad reaching effects for both humans and wildlife.

References

- Almasi, B., Beziars, P., Roulin, A., & Jenni, L. (2015). Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. *Oecologia*, 179(1), 89–101.
<https://doi.org/10.1007/s00442-015-3318-2>
- Bessa, E., Geffroy, B., & Goncalves-De-Freitas, E. (2017). Tourism impact on stream fish measured with an ecological and a behavioural indicator. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 27(6), 1281–1289. <https://doi.org/10.1002/aqc.2804>
- Broekhuis, F. (2018). Natural and anthropogenic drivers of cub recruitment in a large carnivore. *Ecology and Evolution*, 8(13), 1–8. <https://doi.org/10.1002/ece3.4180>
- Christiansen, F., Lusseau, D., Stensland, E., & Berggren, P. (2010). Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endangered Species Research*, 11, 91–99. <https://doi.org/10.3354/esr00265>
- Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., & Harvey, G. M. (2013). Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the Southern stingray, *Dasyatis americana*. *PLoS ONE*, 8(3): e59235. <https://doi.org/10.1371/journal.pone.0059235>
- Creel, S., & Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton, NJ: Princeton University Press.
- Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C. Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE*, 10(5): e0126373.
<https://doi.org/10.1371/journal.pone.0126373>

- Davis, M. L., Kelly, M. J., & Stauffer, D. F. (2011). Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. *Animal Conservation*, 14, 56–65.
<https://doi.org/10.1111/j.1469-1795.2010.00389.x>
- Dillon, A., & Kelly, M. J. (2007). Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx*, 41(4), 469–477.
<https://doi.org/10.1017/S0030605307000518>
- Dudley, J. P., Criag, G. C., Gibson, D. St. C., Haynes, G., & Klimowicz, J. (2001). Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, 39, 187–194. <https://doi.org/10.1046/j.0141-6707.2000.00297.x>
- Dunn, J. C., Hamer, K. C., & Benton, T. G. (2010). Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. *Journal of Applied Ecology*, 47(5), 994–1002.
<https://doi.org/10.1111/j.1365-2664.2010.01856.x>
- French S. S., DeNardo, D. F., Greives, T. J., Strand, C. R., & Demas, G. E. (2010). Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior*, 58(5), 792–799.
<https://doi.org/10.1016/j.yhbeh.2010.08.001>
- French, S. S., Neuman-Lee, L. A., Terletzky, P. A., Kiriazis, N. M., Taylor, E. N., & DeNardo, D. F. (2017). Too much of a good thing? Human disturbance linked to ecotourism has a "dose-dependent" impact on innate immunity and oxidative stress in marine iguanas, *Amblyrhynchus cristatus*. *Biological Conservation*, 210, 37–47.
<https://doi.org/10.1016/j.biocon.2017.04.006>

- Gusset, M., Maddock, A. H., Gunther, G. J., Szykman, M., Slotow, R., Walters, M., & Somers, M. J. (2008). Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation*, 17(1), 83–101.
<https://doi.org/10.1007/s10531-007-9232-0>
- Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. *Biotropica*, 42(1), 126–133. <https://doi.org/10.1111/j.1744-7429.2009.00544.x>
- Heinmeyer, K., Squires, J., Hebblewhite, M., O’Keefe, J. J., Holbrook, J. D., & Copeland, J. (2019). Wolverines in winter: indirect habitat loss and functional responses to backcountry recreation. *Ecosphere*, 10(2): e02611. <https://doi.org/10.1002/ecs2.2611>
- Higginbottom, K., Northrope, C., & Green, R. (2001). *Positive effects of wildlife tourism on wildlife, Wildlife Tourism Research Report Series: No. 6 Status Assessment of Wildlife Tourism in Australia Series*, Cooperative Research Centre for Sustainable Tourism.
- Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE*, 12(10), 1–20.
<https://doi.org/10.1371/journal.pone.0186679>
- Kruger, O. (2005). The role of ecotourism in conservation: panacea or Pandora's box? *Biodiversity and Conservation*, 14(3), 579–600.
<https://doi.org/10.1007/s10531-004-3917-4>
- Ladle, A., Steenweg, R., Shepherd, B., & Boyce, M. S. (2018). The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PLoS ONE*, 13(2): e0191730. <https://doi.org/10.1371/journal.pone.0191730>

- Lindsey, P. A., Alexander, R. R., du Toit, J. T., & Mills, M. G. L. (2005). The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biological Conservation*, 123, 339–348.
<https://doi.org/10.1016/j.biocon.2004.12.002>
- Loveridge, A. J., Kuiper, T., Parry, R. H., Sibanda, L., Hunt, J. H., Stapelkamp, B., ... Macdonald, D. W. (2017). Bells, bomas and beefsteak: complex patterns of human-predator conflict at the wildlife-agropastoral interface in Zimbabwe. *PeerJ*, 5: e2898 <https://doi.org/10.7717/peerj.2898>
- Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., & Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biological Conservation*, 215, 132–141. <https://doi.org/10.1016/j.biocon.2017.07.013>
- Maddock, A. H., & Mills, M. G. L. (1994). Population characteristics of African wild dogs *Lycaon pictus* in the Eastern Transvaal Lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67(1), 57–62.
[https://doi.org/10.1016/0006-3207\(94\)90009-4](https://doi.org/10.1016/0006-3207(94)90009-4)
- Marion, J. L., Leung, Y., Eagleston, H., & Burroughs, K. (2016). A review and synthesis of recreation ecology research findings on visitor impacts to wilderness and protected natural areas. *Journal of Forestry*, 114(3), 352–362. <http://doi.org/10.5849/jof.15-498>
- Marnewick, K., Ferreira, S. M., Grange, S., Watermeyer, J., Maputla, N., & Davies-Mostert, H. T. (2014). Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PloS ONE*, 9(1), e86265. <https://doi.org/10.1371/journal.pone.0086265>

- Marzano, M., & Dandy, N. (2012). Recreationist behaviour in forests and the disturbance of wildlife. *Biodiversity and Conservation*, 21, 2967–2986.
- Merson, S. D., Dollar, L. J., Tan, C. K. W., & Macdonald, D. W. (2019). Activity patterns of sympatric living exotic and endemic carnivores (the fosa) in Western Madagascar's deciduous forests. *Journal of Zoology*, 307, 186–194. <https://doi.org/10.1111/jzo.12630>
- Mhlanga, M., Ramesh, T., Kalle, R., Madiri, T. H., & Downs, C. T. (2018). Spotted hyaena (*Crocuta crocuta*) habitat occupancy in a national park, hunting area and private ranch in western Zimbabwe. *African Journal of Ecology*, 56, 818–827.
<https://doi.org/10.1111/aje.12567>
- Miller, J. R. B., Pitman, R. T., Mann, G. K. H., Fuller, A. K., & Balme, G. A. (2018). Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. *Journal of Animal Ecology*, 87, 1709–1726.
<https://doi.org/10.1111/1365-2656.12883>
- Monz, C. A., Pickering, C. M., & Hadwen, W. L. (2013). Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. *Frontiers in Ecology and the Environment*, 11(8), 441–446.
<https://doi.org/10.1890/120358>
- Mugerwa, B., du Preez, B., Tallents, L. A., Loveridge, A. J., & Macdonald, D. W. (2017). Increased foraging success or competitor avoidance? Diel activity of sympatric large carnivores. *Journal of Mammalogy*, 98(5), 1443–1452.
<https://doi.org/10.1093/jmammal/gyx090>

- Mugerwa, B., Sheil, D., Ssekiranda, P., van Heist, M., & Ezumea, P. (2013). A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology*, 51, 21–31. <https://doi.org/10.1111/aje.12004>
- Müllner, A., Linsenmair, K. E., & Wikelski, M. (2004). Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, 118, 549–558. <https://doi.org/10.1016/j.biocon.2003.10.003>
- Nortje, G. P., van Hoven, W., & Laker, M. C. (2012). Factors affecting the impact of off-road driving on soils in an area in the Kruger National Park, South Africa. *Environmental Management*, 50(6), 1164–1176. <https://doi.org/10.1007/s00267-012-9954-y>
- Olson, L. E., Squires, J. R., Roberts, E. K., Ivan, J. S., & Hebblewhite, M. (2018). Sharing the same slope: behavioral responses of a threatened mesocarnivore to motorized and nonmotorized winter recreation. *Ecology and Evolution*, 8, 8555–8572. <https://doi.org/10.1002/ece3.4382>
- Rasmussen, G. S. A. (1999). Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: A case study. *Biological Conservation*, 88, 133–139. [https://doi.org/10.1016/S0006-3207\(98\)00006-8](https://doi.org/10.1016/S0006-3207(98)00006-8)
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D. W. (2008). Achilles heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. <https://doi.org/10.1086/590965>
- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286(3), 232–242. <https://doi.org/10.1111/j.1469-7998.2011.00874.x>

- Reynolds, P. C., & Braithwaite, D. (2001). Towards a conceptual framework for wildlife tourism. *Tourism Management*, 22(1), 31–42.
[https://doi.org/10.1016/s0261-5177\(00\)00018-2](https://doi.org/10.1016/s0261-5177(00)00018-2)
- Rovero, F., & Zimmermann, F. (Eds.). (2016). *Camera Trapping for Wildlife Research*. Exeter, UK: Pelagic Publishing.
- Safari Bookings (Hwange NP). (2019). *Weather & Climate – Hwange NP*. Retrieved from <https://www.safaribookings.com/hwange/climate>
- Scholten, J., Moe, S. R., & Hegland, S. J. (2018). Red deer (*Cervus elaphus*) avoid mountain biking trails. *European Journal of Wildlife Research*, 64(8).
<https://doi.org/10.1007/s10344-018-1169-y>
- Shumba, T., Montgomery, R. A., Sillero-Zubiri, C., & Rasmussen, G. S. A. (2017). Morphological variation of wild dogs across Africa. *International Journal of Zoology and Applied Biosciences*, 2(3), 145–154.
- Spaul, R. J., & Heath, J. A. (2016). Nonmotorized recreation and motorized recreation in shrub-steppe habitats affects behavior and reproduction of golden eagles (*Aquila chrysaetos*). *Ecology and Evolution*, 6, 8037–8049. <https://doi.org/10.1002/ece3.2540>
- Steinmetz, J. T. (2017, July 21). Tourism development and conservation: challenges and opportunities. *eTurboNews*. Retrieved from <https://www.eturbonews.com/160138/tourism-development-conservation-challenges-opportunities>.
- Storch, I. (2013). Human disturbance of grouse—why and when? *Wildlife Biology*, 19(4), 390–403. <https://doi.org/10.2981/13-006>

- van der Meer, E., Mpofu, J., Rasmussen, G. S. A., & Fritz, H. (2013). Characteristics of African wild dog natal dens selected under different interspecific predation pressures. *Mammalian Biology*, 78(5), 336–343. <https://doi.org/10.1016/j.mambio.2013.04.006>
- van der Ree, R., Smith, D. J., & Grilo, C. (Eds.). (2015). *Handbook of Road Ecology*. Hoboken, NJ: Wiley-Blackwell. <https://doi.org/10.1002/9781118568170>
- Vickers, N. J. (2000). Mechanisms of animal navigation in odor plumes. *Biological Bulletin*, 198(2), 203–212. <https://doi.org/10.2307/1542524>
- Welch, R. J., Grant, T., & Parker, D. M. (2019). Using camera traps to generate a species inventory for medium-sized and large mammals in South West Zimbabwe. *African Journal of Wildlife Research*, 49, 89–99. <https://doi.org/10.3957/056.049.0089>
- Wilkinson, I. (1995). *The 1994/1995 wild dog photographic survey*. South African National Parks unpublished report, South African National Parks, Skukuza.
- Wolf, I. D., & Croft, D. B. (2010). Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. *Applied Animal Behaviour Science*, 126, 75–84. <https://doi.org/10.1016/j.applanim.2010.06.001>
- Wolf, I. D., Croft, D. B., & Green, R. J. (2019). Nature conservation and nature-based tourism: a paradox? *Environments*, 6. <https://doi.org/10.3390/environments6090104>
- World Tourism Organization. (2014). *Towards measuring the economic value of wildlife watching tourism in Africa: briefing paper*. Madrid: World Tourism Organization.
- Zimbabwe Parks and Wildlife Management Authority (ZPWMA). (2017a). Victoria Falls. Retrieved from <http://zimparks.org/parks/national-parks/victoria-falls/>

Zimbabwe Parks and Wildlife Management Authority (ZPWMA). (2017b). Investment Prospectus. Retrieved from <http://zimparks.org/wp-content/uploads/2015/11/Zimbabwe-Prospectus-Parks-Website.pdf>

Chapter V: Feeding Regimen and Growth Comparison in Two Related African Painted Dog (*Lycaon pictus*) Litters

Abstract

There is a lack of published studies on feeding regimens and growth in captive painted dog populations. Captive animals are expected to accurately represent their wild counterparts, yet captivity has been shown to alter the morphology of various species, which may potentially be related to diet and/or feeding regimen. Here I present a case study evaluating the influence of two feeding regimens (free feed and controlled feed) on weight and morphometric measurements of two related painted dog litters (i.e., same sire, sibling dams). Both litters were fed the same diet, but beginning at approximately 10 weeks of age, Litter A's food was freely available throughout the day (i.e., free feed), whereas Litter B was fed at specific times of day (i.e., controlled). Ten physical measurements were obtained at 10 and 14-week pup wellness checks. Morphometric measurements between litters were comparable for body length, ear height, head circumference, and muzzle length. Conversely, hind leg/body length ratios, the differentials between front and hind limbs and body length, and mean body mass differed significantly. Body mass means were greater for Litter A, and Litter B's hind leg lengths were longer relative to body and front leg length. These results indicate that there is a potential influential relationship between how an animal is fed and their growth. If this is the case, altered morphometrics of captive animals that will be released into the wild, or starvation conditions in free-ranging packs during critical growth periods, could have profound unknown consequences. More information relating to feeding regimens, diet, and growth is needed for both *in-situ* and *ex-situ* painted dogs to improve husbandry practices for captive individuals and conservation efforts for free-ranging populations.

Keywords: carnivore, husbandry, diet, *Lycaon pictus*, African wild dog, development, Carnivora

Introduction

As zoos and captive breeding programs provide a source of genetic stock for wild populations, it is important that captive individuals receive proper care so they can accurately represent their wild counterparts. Although zoological institutions are attempting to maintain genetic diversity (Marsden et al., 2013), captivity has been demonstrated to alter morphology in carnivores (Curtis, Orke, Tetradis, & van Valkenburgh, 2018; Hartstone-Rose, Selvery, Villari, Atwell, & Schmidt, 2014) and other groups (Dierenfeld, 1997; O'Regan & Kitchener, 2005). This is problematic as altered morphology of individuals targeted for release or reintroduction could prove detrimental for both individuals and populations in ways that are not fully understood.

Early dietary management of captive animals attempted to replicate wild diets, but focused more on short-term goals such as keeping animals alive rather than long-term health, growth, and reproduction (Dierenfeld, 1997). Advances in nutritional knowledge improved feeding protocols by accounting for important aspects such as life stage (e.g., maintenance, lactation, disease; Dierenfeld, 1997; Irwin, Stoner, & Cobaugh, 2013), and by replicating the chemical components of natural prey (Hartstone-Rose, Selvey, Villari, Atwell, & Schmidt, 2014). Although dietary components have generally improved, implementing standardized dietary requirements and feeding regimens among zoological institutions and species is difficult due to varying needs of individuals within a species. Despite recommendations that captive animal diets are developed according to individual and species nutritional requirements, feeding ecology, and natural history (AZA Canid TAG, 2012, p. 28), choice of food items is often constrained by funding, practical considerations such as convenience, and an institution's level of comfort and familiarity (Hill, Huskisson, Weigel, & Mendelson III, 2019).

Quality nutrition is vital, but is *how* and *when* an animal is fed as important as *what* an animal is fed? When African lions (*Panthera leo*) were switched from routine feeding schedules to a fast/gorge schedule, the lions lost weight (making their weight comparable with the weight of wild lions), and their digestibility of fat and protein increased (Altman, Gross, & Lowry, 2005). Similar differences or changes have also been observed in reptiles. Boas (*B. constrictor*), for example, fed 20% of their body mass on a bi-weekly basis grew larger and faster than a group fed 10% of their body mass on a weekly basis (Hill et al., 2019). It is unclear how, or if, the larger and faster growth affected the boas in the short or long-term, but these case studies lend support to the potential influence of feeding strategies (e.g., frequency and volume) on the fitness and growth of various species (Hill et al., 2019).

Developing optimal feeding protocols for carnivores can be challenging (Altman et al., 2005), and many institutions learn through trial and error based on recommendations from veterinary and nutritional professionals (Meuffels et al., 2019). The implications are especially important for species such as the endangered African painted dog (*Lycaon pictus*), where knowledge gaps regarding potential relationships between diet, feeding protocols, and growth exist. Painted dogs, also known as African wild dogs, are one of Africa's most endangered carnivores (Woodroffe & Sillero-Zubiri, 2012). As cooperative hunters and breeders, each pack member is crucial to foraging activities that are vital for raising young and pack survival (Courchamp & Macdonald, 2001; Courchamp, Rasmussen, & Macdonald, 2002; Creel, 2001). Nomadic for most of the year, painted dogs are stationary for the approximately 12-week denning season. They hunt multiple times a day (i.e., dawn, dusk, full moon; Rasmussen & Macdonald, 2012; Rasmussen, Gusset, Courchamp, & Macdonald, 2008), with typical prey including ungulates such as impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), and

duiker (*Sylvicapra grimmia*; Rasmussen, 1999). Energetic costs are extremely high during this time due to the need to quickly raise pups and become nomadic again (Rasmussen et al., 2008). Evolutionary adaptations such as rapid maturation that includes quick body and leg length growth to achieve quick pup mobility, as well as optimal adult anatomical proportions needed to successfully chase and capture prey, are likely critical features for long-term survival. In fact, it is assumed that most canid species have evolved similar adaptations in their growth rates and body proportions (Hildebrand, 1952).

In North American facilities, most painted dogs are fed a “nutritionally complete raw meat-based” diet on a daily basis (AZA Canid TAG, 2012, p. 30). Supplemental items such as bones, rabbits, mice, and deer carcasses are also offered (AZA Canid TAG, 2012; Cloutier & Packard, 2014). No specific feeding protocols are provided for neonates as it is expected that nutritional needs are met by nursing females, although regular assessments (including morphometric measurements) of young as they grow are recommended (AZA Canid TAG, 2012; Bell et al., 2012). Bell et al. (2012) noted that feeding protocols differ between North America and other parts of the world, but that many facilities use *ad libitum* feeding (i.e., food is freely available rather than offered at specific times). The assumption is that animals will self-regulate to obtain adequate nutrition.

Animals not receiving nutritional support for appropriate growth at critical stages could have their overall growth as adults, and thus their fitness and survival in both captivity and the wild, adversely impacted. For painted dogs, empirical studies on their feeding and growth in zoos could facilitate a greater understanding of their development needs. One institution compared the influence of hand feeding and group feeding protocols on the weight and morphometrics of female siblings from successive litters (Gorsuch & Kelly, unpublished data).

They found that the pups that were started on meat at 6 weeks of age and fed as a pack weighed more and had longer body, front, and hind limb measurements than the individuals not fed this way. Here I investigated the influence of two different feeding regimens (free feed and controlled feed) on the morphometrics and weight of two related litters of painted dogs. The goal was to learn how to improve conditions for raising painted dogs in captivity for overall health and fitness, as well as for if the need arises to release individuals into the wild, as has been done for other species (Britt et al., 2004; Sanz & Grajal, 1998; Tutin et al., 2001).

Methods

Study Site

The Endangered Wolf Center (EWC) is located in eastern Missouri. EWC's landscape consists of old growth hardwood forest and rolling hills, with sycamore, cottonwood, hickory, and oak as some of the dominant tree species. Temperatures range from below freezing during winter to over 32° C (90° F) in the hot, dry summer season. Mean annual precipitation averages around 9.14 cm (3.6 in; Decker, 2020).

Litters

Two litters of painted dogs were born at EWC in 2018: Litter A (13 puppies; 8 females, 5 males) was born on November 16, and Litter B (10 puppies; 5 females, 5 males) was born on November 20. The sire of both litters was born on September 14, 2012, and the sibling dams were born on June 23, 2014. All three adults lived together within the same enclosure (Figure 5-1). Litter A's dam went into labor first and selected the den on the right side of the enclosure (Figure 5-1). Litter B's dam was then contained on the left side (Figure 5-1) where she gave birth four days later. Aggression between the dams prevented reintroduction of all individuals into one cohesive pack. In lieu of one pack, the sire was shifted between enclosures on average every 1–3 days to encourage social interaction between both females and their litters.

Enclosures

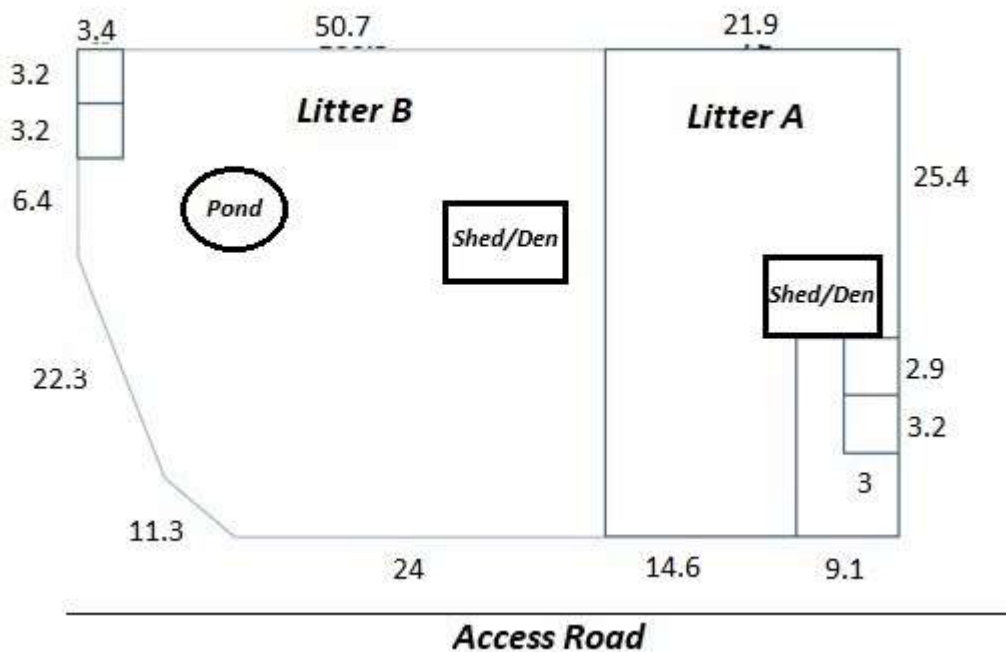
The painted dog exhibit consisted of two adjoining enclosures separated by a chain link fence and two access gates (Figure 5-1). The front of Litter A's enclosure faced an access road, with the remaining two sides facing Mexican gray wolf (*Canis lupus baileyi*) and Maned Wolf (*Chrysocyon brachyurus*) enclosures. Litter A's enclosure included a tunnel, hill, trees, and fallen logs. The front and a portion of one side of Litter B's enclosure faced the access road and the rear faced a Mexican gray wolf enclosure. It included a tree, pond, and fallen logs. Both

enclosures contained sheds/dens and holding areas (represented by two adjacent rectangles in Figure 5-1). Substrate consisted of varying degrees of bare ground, grass, leaf litter, and snow throughout the study period.

Figure 5-1

Diagram of the Endangered Wolf Center's African painted dog enclosures with approximate measurements (in meters). Features within the enclosures are representative and not to scale.

Diagram courtesy of Erin Connett.



Diet

Pups were weaned around three weeks of age when adults began regurgitating food for them. Beginning at approximately 10 weeks of age, the same diet that consisted of a precalculated combination of meat items and Mazuri Exotic Canine Dry Dog Food (also referred to as chow) was free fed to Litter A and fed in a controlled manner (i.e., fed at specific times of the day) to Litter B. The formula, $ME \text{ (kcal/d)} = 130 \times BW \text{ (kg)}^{0.75}$, was used as a general

reference when determining the amount of food needed per pup (D. Schmidt, personal communication, 2020). Initially, Litter A (13 pups) was offered a daily total of approximately 3600 g of meat items and 900 g of chow. Litter B (10 pups) received approximately 2300 g of meat items and 900 g of chow on a daily basis. As the pups matured, increases in diet volume were based on 5–7% of their average body weight. Appetite consumption (i.e., voracity) and outside temperatures (which ranged from -21 to 22°C [-6 to 71°F]) during the study period) were also factored into their feeding regimens. For example, pups were offered extra pre-weighed food when temperatures were below freezing.

Meat items for both litters consisted of the following: 80% Nebraska Classic Canine diet, 17% whole prey items cut into pieces (primarily rabbit and guinea pig, but venison and bison were included as well), and 3% beef fat cut into bite-sized cubes. Beef and pork were added occasionally. All food (including carcasses or bones) was weighed and recorded before feedings, as was any food not consumed. Food requirements were calculated based on individual pup needs, but fed at the aggregate litter level, so exact volumes consumed by individual pups at each feeding are unknown. Meat items were only offered by keepers during twice daily training sessions to Litter B. In contrast, Litter A was offered meat by hand during training sessions and had access to meat items throughout the day.

Litter A Feeding Protocol

As noted above, a portion of the daily allowance of meat items was offered by keepers during training sessions for both litters. In addition, the remainder of meat items, along with chow, was always freely available to Litter A on a food tray. The tray was checked/replenished twice a day (9:30 am and 2:30 pm). At the 9:30 am check, food was replenished, and any remaining chow and meat left in the tray was weighed, recorded, and left there. If there were no leftovers, pups were offered handfed meat items until full, after which at least 2.3 kg (5 lbs) of

Nebraska Classic Canine diet was weighed and left in the food tray until the 2:30 pm feeding. At the latter feeding, any food items in the tray were weighed and left in the tray. If the tray was empty/near empty, more chow was weighed and added. Again, if the tray was empty, pups were offered handfed pre-weighed meat items until full, after which two pounds of chow was left in the tray overnight. Any food remaining in the tray in the morning was removed.

Litter B Feeding Protocol

The daily allowance of chow and meat was divided into two portions and fed at approximately 10:30 am and 2:30 pm, each coinciding with the litter's daily training sessions. Two pounds of chow was placed in a food tray after the morning feeding/training session with handfed meat items had ended. Any remaining meat items from the morning feeding were taken away and stored, and then offered again by hand at the afternoon feeding. In addition, any leftover chow was weighed, recorded, and left out until the afternoon feeding. If there were meat items left over from the 2:30 pm feeding, they were weighed and used as part of the next day's diet.

Data Collection

Wellness checks

Three wellness checks were performed when the pups were approximately 7, 10, and 14 weeks of age. Pups were weighed at each wellness check and morphometric measurements were obtained at 10 and 14 weeks. After containing the adults, EWC staff and volunteers captured each litter separately, placing multiple individuals from the same litter together in portable kennel crates. Crates were transported to a work area in a large, quiet building where the wellness checks (e.g., physical exam, weight, vaccinations) and morphometric measurements were completed. The work area was divided into two sections (one for Litter A, one for Litter B) prior to the arrival of the pups to limit separation time and decrease handling time and stress.

Morphometric measurements

Prior to the pups arriving, instructions and reference measurement charts (Figure 5-2) were provided to participants who obtained morphometric measurements (Table 5-1). Two handlers manually restrained each pup while one person took measurements using a measuring tape. A cloth was placed over each pup's eyes to minimize stimulation during measurements. Each measurement was rounded to the nearest centimeter (cm) for efficiency and verbally relayed to, and confirmed by, an assigned data recorder for documentation. Once measured, pups were placed in carriers with their littermates in a quiet area. All pups were transported back to their enclosures as soon as possible following measurement of the last pup.

Figure 5-2

Morphometric measurements obtained for each painted dog pup during 10 and 14-week wellness checks at the Endangered Wolf Center. Image courtesy of Greg Rasmussen.

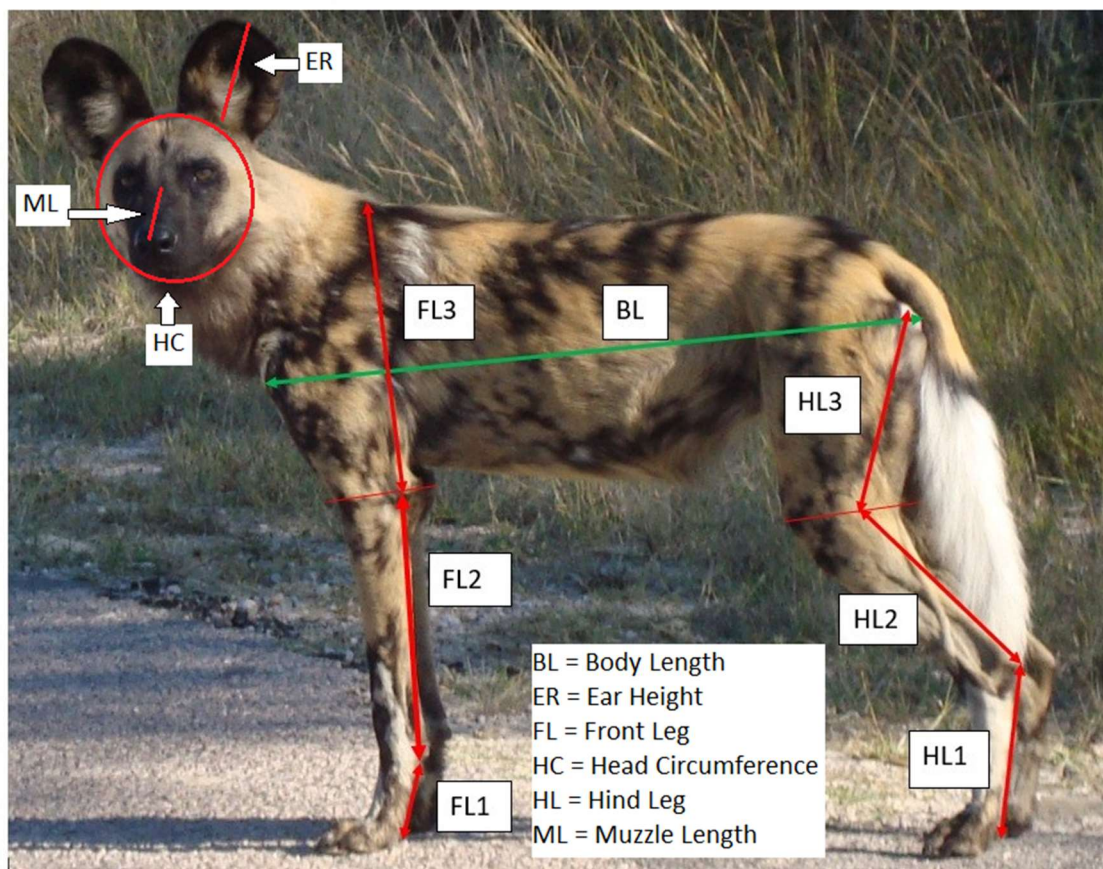


Table 5-1

Definitions of morphometric measurements obtained for each painted dog pup at 10 and 14-week wellness checks at the Endangered Wolf Center

Abbreviation	Definition	Points of Measurement
BL	Body Length	point of front shoulder to sacroiliac process under base of tail
FL1	Front Leg Measurement 1	ventral surface of paw pad to rear carpal joint
FL2	Front Leg Measurement 2	rear carpal joint to back of elbow joint
FL3	Front Leg Measurement 3	back of elbow joint to dorsal point of scapula
HL1	Hind Leg Measurement 1	ventral surface of paw pad to rear of hock
HL2	Hind Leg Measurement 2	rear of hock to mid-stifle joint
HL3	Hind Leg Measurement 3	mid-stifle joint to tip sacroiliac process
ER	Ear Height	middle of base of front of ear to highest point of ear
HC	Head Circumference	start and stop at midpoint between ears following base of ears and mandible
ML	Muzzle Length	base of muzzle near eyes to tip of nose

Data Analysis

Morphometric measurements

Ten morphometric measurements were obtained for each pup (Table 5-1). The ER, HC, and ML measurements were selected as they were generally quickly and easily obtained, whereas BL and front and hind limb length measurements were chosen because they provided discrete measurement points that can be easily replicated and compared. The following metrics

were included in the analysis: BL, ER, HC, ML, FL/BL, HL/BL, and FL-HL/BL (Tables 5-1 and 5-2).

Table 5-2

*Morphometric measurement definitions for three of five response variables used in analyses of *Lycaon pictus* belly scores*

Abbreviation	Definition	Points of Measurement
TFL	Total Front Leg	sum of FL1, FL2, and FL3
THL	Total Hind Leg	sum of HL1, HL2, and HL3
FL-HL/BL	Front Leg/Hind Leg Differential	difference between TFL and THL divided by BL
FL/BL	Front Leg/Body Length Differential	front leg divided by body length
HL/BL	Hind Leg/Body Length Differential	hind leg divided by body length

Morphometric measurements were visually assessed for normality. A t-test was used to evaluate whether there was an effect of sex on growth (i.e., a difference in measurements and proportions between males and females). Mixed effects models were run to test whether each morphometric measurement, the response variable, was related to predictor variables litter (and hence, feeding regimen), age, and the interaction between the two to indicate differences between the litters in the growth of pups over time. Separate models were created for each of the seven metrics listed above. A relationship between each pup's measurements over time was assumed (i.e., if a pup was larger at birth, it would remain so over time); pups were thus treated as a random effect, whereas time (week) was treated as a fixed effect. All analyses were conducted using IBM SPSS Statistics 26 ($\alpha = 0.05$).

Results

There was no effect of sex ($t = -1.560$, $df = 56.563$, $p = 0.124$), therefore, sex was not included in the mixed effects models. Measurements for body length (BL), ear height (ER), head circumference (HC), and muzzle length (ML) were comparable between the litters (Table 5-3). As expected, measurements increased significantly between wellness checks as pups grew (Table 5-3).

Table 5-3

Comparison of morphometric means and weights between painted dog Litter A and Litter B at 10 and 14-week pup wellness checks and results of the fixed effects from the mixed effects models

	Age (weeks)	Litter A Measurement Mean (cm)	Min/Max (cm)	Std. Error	Litter B Measurement Mean (cm)	Min/Max (cm)	Std. Error	Effect of Litter	Effect of Age	Effect of Litter and Age Interaction
Body length	10	38.15	32/45	0.878	37.3	32.5/41	1.001	$F_{1,21} = 1.639$, $p = 0.214$	$F_{1,21} = 212.953$, $p = 0.000$	$F_{1,21} = 0.705$, $p = 0.410$
	14	49.04	43/53		47.00	43.5/49				
Ear height	10	9.19	8.25/10	0.190	8.98	8/10	0.216	$F_{1,21} = 0.019$, $p = 0.892$	$F_{1,21} = 115.790$, $p = 0.000$	$F_{1,21} = 1.179$, $p = 0.290$
	14	10.85	10/11.5		11.00	10/12.5				
Head circumference	10	30.09	28/33	0.347	29.80	28.5/31.5	0.396	$F_{1,21} = 1.675$, $p = 0.210$	$F_{1,21} = 363.180$, $p = 0.000$	$F_{1,21} = 1.165$, $p = 0.293$
	14	35.58	34/37.5		34.70	32/37				
Muzzle length	10	13.12	12/15	0.282	12.60	11.5/14	0.321	$F_{1,21} = 0.770$, $p = 0.390$	$F_{1,21} = 49.060$, $p = 0.000$	$F_{1,21} = 0.693$, $p = 0.415$
	14	14.77	13/16		14.70	13/18				
Front leg/Body length	10	0.974	0.848/1.109	0.020	0.967	0.902/1.046	0.023	$F_{1,21} = 0.006$, $p = 0.938$	$F_{1,21} = 0.342$, $p = 0.565$	$F_{1,21} = 0.183$, $p = 0.673$
	14	0.954	0.855/1.116		0.964	0.906/1.106				
Hind leg/Body length	10	0.990	0.775/1.138	0.024	0.969	0.902/1.076	0.027	$F_{1,21} = 1.710$, $p = 0.205$	$F_{1,21} = 0.001$, $p = 0.972$	$F_{1,21} = 9.001$, $p = 0.007$
	14	0.929	0.839/1.058		1.029	0.958/1.103				
Front leg - Hind leg/Body length	10	-0.016	-0.156/0	0.018	-0.002	-0.039/0	0.020	$F_{1,21} = 3.510$, $p = 0.075$	$F_{1,21} = 0.330$, $p = 0.572$	$F_{1,21} = 7.911$, $p = 0.010$
	14	0.025	-0.048/0		-0.064	-0.195/0.010				
Weight (in kg)	7	3.79	3.44/4.17	0.376	3.56	2.90/4.08	0.429	$F_{1,21} = 11.510$, $p = 0.003$	$F_{1,21} = 1529.660$, $p = 0.000$	$F_{1,21} = 29.642$, $p = 0.000$
	10	5.98	4.71/6.71		5.77	4.71/6.62				
	14	10.98	9.52/12.06		9.19	7.52/11.06				

Front leg/body length (FL/BL) ratios were not significantly affected by litter (i.e., feeding regimen), age, or the interaction of litter and age (Table 5-3). Front legs of pups were consistent in proportion to their body across litter and time (Table 5-3). In contrast, hind leg/body length growth and differences between limb lengths/body lengths, were significantly different with the interaction of litter and age (Table 5-3, Figures 5-3 and 5-4). This presented as Litter B's hind legs being longer than their front legs when compared to Litter A (Figures 5-5 and 5-6). In addition, litter, age, and the interaction of litter and age, all had significant effects on differences in mean weights (Table 5-3).

Figure 5-3

Interaction plot comparing painted dog pup means of HL/BL (ratio of THL [total hind leg] divided by BL [body length]) between Litter A (free feed) and Litter B (controlled feed) at 10 and 14-week pup wellness checks

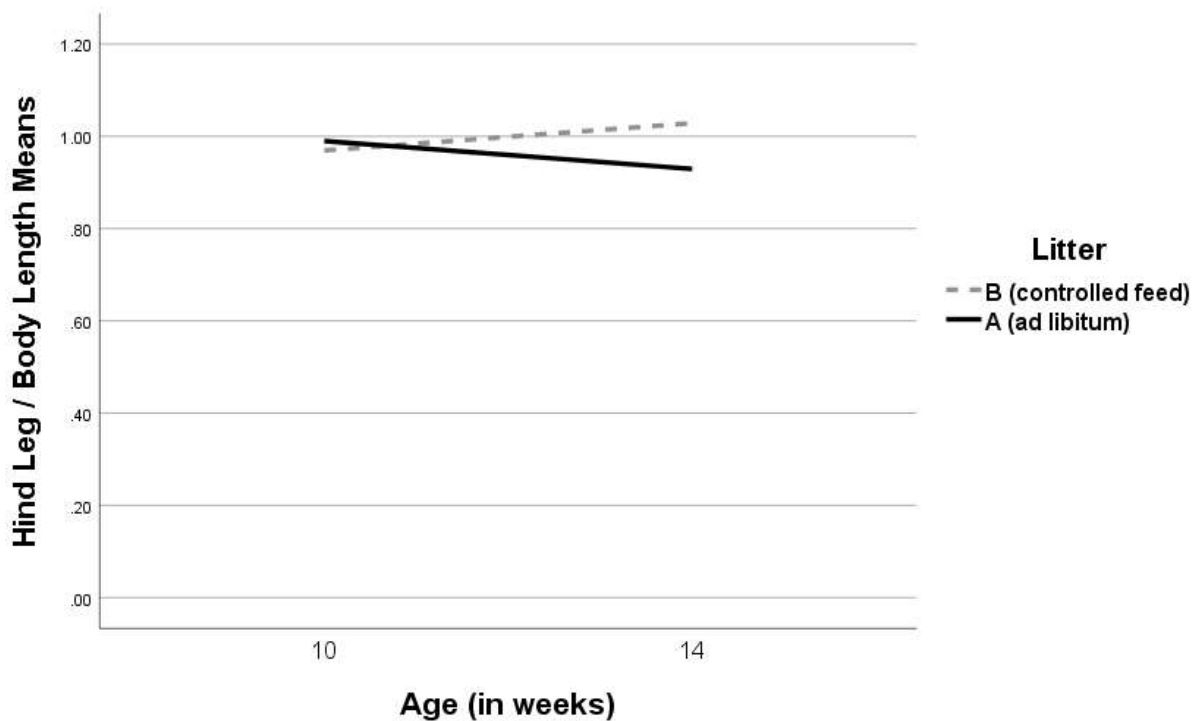


Figure 5-4

Interaction plot comparing painted dog pup means of FL-HL/BL (difference between TFL [total front leg] and THL [total hind leg] divided by BL [body length]) between Litter A (free feed) and Litter B (controlled feed) at 10 and 14-week pup wellness checks

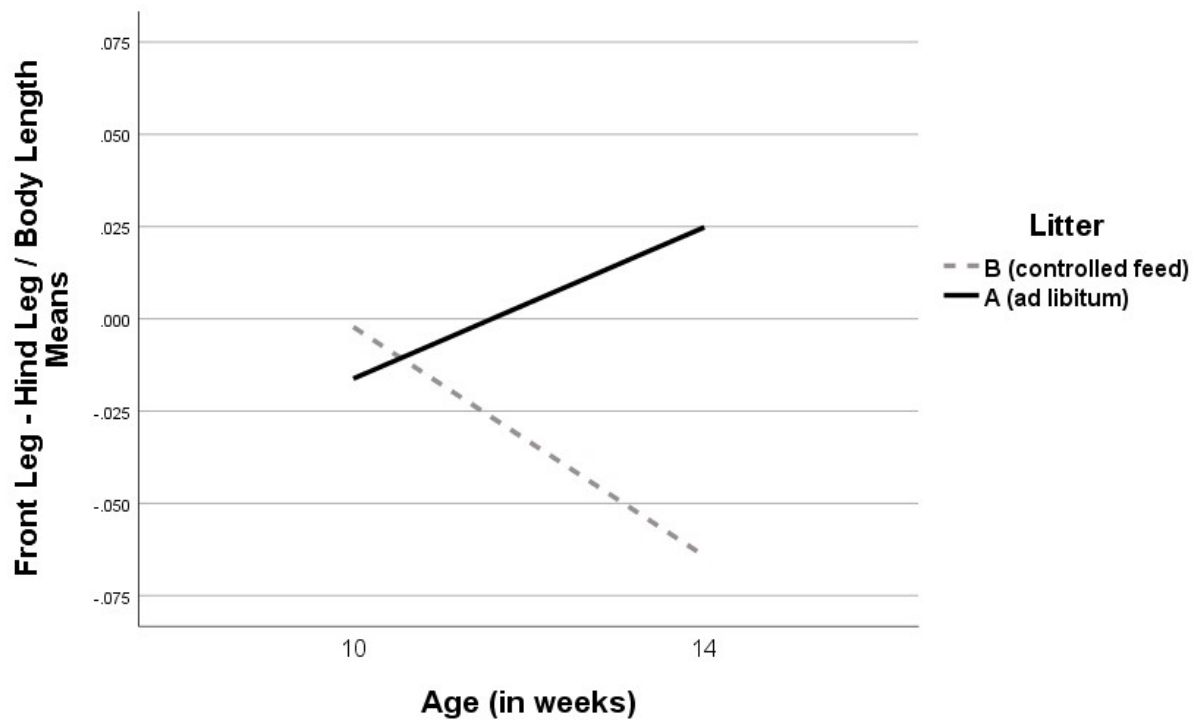
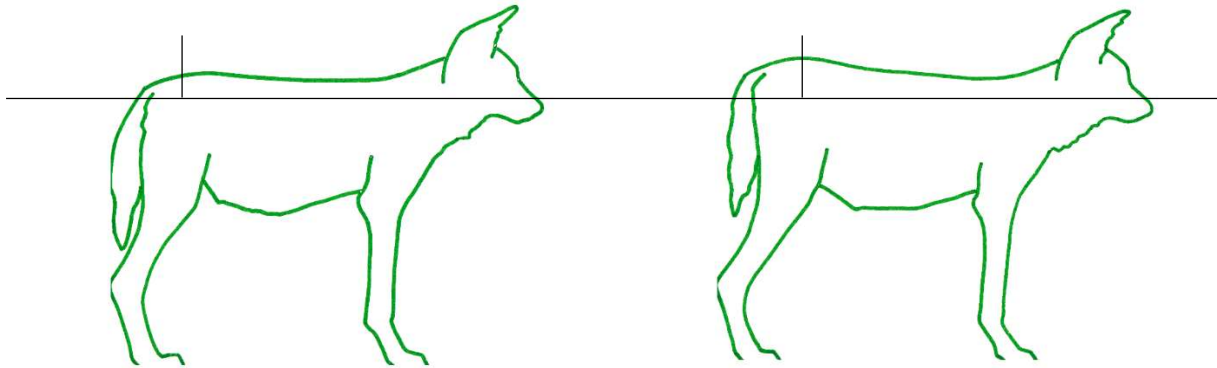


Figure 5-5

Comparison of painted dog pup body and limb lengths based on morphometric measurements obtained from Litter A (on left; free feed) and Litter B (on right; controlled feed) at 10-week pup wellness check. Illustrations courtesy of Alison Nicholls.

**Figure 5-6**

Comparison of painted dog pup body and limb lengths based on morphometric means obtained from Litter A (on left; free feed) and Litter B (on right; controlled) at 14-week pup wellness check. Illustrations courtesy of Alison Nicholls.

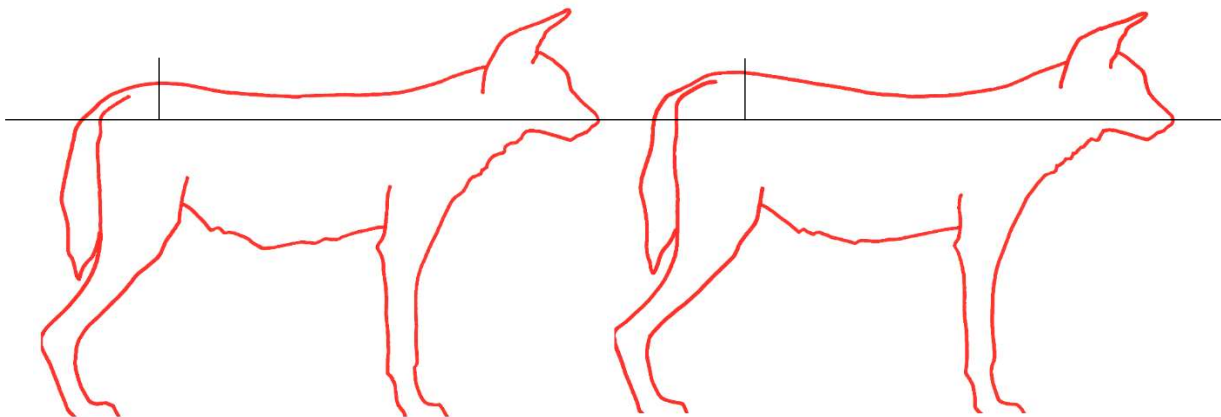


Table 5-4

Comparison of mean weights (in grams) between captive painted dog Litter A and Litter B at 53 and 49 days of age, respectively, and mean weights of North American captive litters born between 1994 and 2017 (total of 503 individuals; Powell, unpublished data)

	Age (in days)	Mean Weight (in grams)	Mean Weight of Previous North American Litters (in grams)
Litter A	53	3790	2761.2
Litter B	49	3560	3095.2

Discussion

This case study investigated feeding regimens and growth between two closely related captive painted dog litters at a North American conservation facility. Painted dog pup morphometric measurements were reported in two previous publications, although the majority of those measurements differ from what is presented in this study. Thomas et al. (2006) measured pinna length, comparable to what is labeled as "ear height" here, and Kenny et al. (2007) measured height, defined as the top of the scapula to the bottom of the foot when placed flat. The latter may be similar to my total front leg measurement, but without knowing more specific measurement points, that remains unclear. Ear height means and significant differences in measurements over time were consistent with Thomas et al. (2006). In addition to Litter A weighing more than Litter B throughout the study period, mean weights of both litters were heavier than those of captive North American pups (total of 503 individuals) in litters born between 1994 and 2017 (Powell, unpublished data). It should be noted however, that the mean weights of the 503 North American painted dog pups is based on all litters of various sizes that occurred between 1994 and 2017, and not only litter sizes that matched the two EWC litters presented here. This may be relevant for growth and development, and requires further study. Because there is a lack of published data on overall growth and body and limb length ratios in captive and free-ranging painted dogs, it is unknown if the measurements in this study are comparable to other individuals or populations.

One sire and two females who were sisters offered a situation where confounding factors such as genetics and environment were decreased, although not fully eliminated, for these two litters. And while this can be considered a strength for this study, the small sample size and brief data collection timeframe were limitations. Regardless, results from this study provide a baseline of information that zoological institutions can build on for future litters of painted dogs, or to use

as an example for other species. If the zoological community chooses to continue collecting this type of data to assist with advancing painted dog husbandry practices, it is strongly recommended that protocols are developed as soon as possible. This will allow for a standardized procedure to be applied across all litters and will enable captive wildlife managers to implement data collection at a younger age to obtain further information related to diet, feeding regimen, and growth. It is understood that there are limited opportunities to conduct physical morphometric measurements throughout an animal's life as sedation is required in many cases. However, as discussed in Chapter III, belly scores allow "quick" health assessments for free-ranging populations, and could for captive individuals as well (across all life stages), with no sedation required. A compilation of varied data such as physical measurements, belly scores, behaviors, and enclosure sizes and features can provide insight on how current husbandry practices can be modified to meet captive painted dog needs, and how captive populations compare to free-ranging populations in the areas of diet, growth, and development.

Diet and appropriate growth are important for the overall health of captive animals, but particularly relevant for captive individuals targeted for reintroduction and free-ranging populations stressed by humans. Studies have shown that captivity played a role in altering morphology in other species (Curtis et al., 2018; Dierenfeld, 1997; Hartstone-Rose et al., 2014; O'Regan & Kitchener, 2005). Although morphological diversity is apparent among wild and domesticated canids, the conformation variations do not always lend themselves to maximum energetic efficiency (Bryce & Williams, 2017). For example, Bryce and Williams (2017) observed that northern dog breeds (e.g., Siberian huskies, Alaskan malamutes, Samoyeds) had lower locomotor costs when trotting compared to other gaits (i.e., walk, gallop); similar to their wild conspecifics, wolves. Other similarities between northern dog breeds and wolves is that

their hind limbs are located closer to their center of mass, allowing for a more upright stance, and relatively flat topline when running, promoting energy efficiency (Bryce & Williams, 2017). In contrast, domestic dog breeds such as hounds and retrievers have wider hip angles and hold their heads in more of an upright position, increasing their locomotor costs (Bryce & Williams, 2017).

As cursorial predators that patrol territories and travel long distances, painted dogs share similar conformations with wolves and northern dog breeds. Despite these similarities, there are differences as well. One example is hindlimb muscular configuration. The painted dog's configuration functionally separates hip flexion and knee extension in a manner that appears to support energy conservation for their nomadic and cursorial lifestyle (Wright, Smith, & Grossman, 2019). These observations support the contention that changes in front or hind limb morphology in painted dogs may affect their center of mass and increase energetic costs when chasing prey and traveling, potentially decreasing fitness and survival (Bryce & Williams, 2017; Kilbourne & Hoffman, 2015). Captive individuals may differ in the amount and/or type of locomotion due to enclosure limitations, raising the question to what extent such conditions might have on them relative to their free-ranging counterparts. Regardless of the extent of the difference, morphological change of this type must be taken into consideration when caring for these animals, particularly if morphological differences are retained as adults.

Bell et al. (2012) suggested that individuals fed *ad libitum* would show higher growth, demonstrated by longer body and limb length. Litter A, the free feed litter, exhibited larger body lengths, however, the difference was not significant. In addition, although Litter A also weighed more than Litter B, this was consistent for all three wellness checks, even before feeding regimen differences were implemented, suggesting that weight differences may not necessarily be attributed to feeding regimen. Both litters demonstrated body and limb length differences over

time, yet Litter B's hind legs were significantly longer relative to their body and front limb length, particularly at the 14-week pup wellness check. This changed their conformation in comparison to Litter A by shifting their center of mass to a more forward and down rather than upright position, altering their stance and running gaits. The difference was less pronounced at the 10-week wellness check, so it is unclear if this difference is influenced by feeding regimen. It is also unknown if or how this morphometric alteration will affect them as adults, but this change in conformation could be detrimental to captive animals, captive animals released into the wild, and free-ranging populations that are not able to adequately feed pups. Potential implications are that painted dogs may not be able to maintain normal running speeds or distances, leading to decreased foraging success and vulnerability to intraguild predators such as lions and spotted hyenas (*Crocuta crocuta*). Further research into how morphological changes may affect health and fitness is required and highly recommended.

As both litters were offered approximately the same amount of food per pup, it is uncertain if the morphological differences observed between litters can be attributed to feeding regimen, level of activity of each litter, genetics, and/or other unknown factors. It does highlight the need for further consideration of factors such as individual/pack differences and/or enclosure guidelines. For example, Litter A's measurements were slightly larger overall, and while both litters engaged in play behavior that included running and wrestling, Litter B was generally more active based on keeper and intern observations. This may be due to personality or other factors, or to the fact that Litter B's enclosure was larger, enabling them to run longer distances for longer periods of time. The difference in engagement in these locomotive behaviors as related to foraging may potentially illustrate the connection between predatory behavior and morphology referenced by Martín-Serra, Figueirido, and Palmqvist (2016) in that limb/body length ratios may

be affected by activity levels and feeding protocols. This may offer one potential explanation for the difference in limb ratios between these two litters.

One male producing simultaneous litters with two sisters offered an opportunity to collect information on the potential relationship between feeding regimen and growth of painted dogs at a single conservation facility. While the nature of this opportunity allowed influential factors such as genetic and environmental variation to be reduced, it does not eliminate the effects of these and other internal or external factors. These results do however indicate a need for more information relating to diet, feeding regimens, and growth in both captive and free-ranging painted dog populations. Future research should include studying when/if *ad libitum* diets should be offered, and comparing growth rates among *ex-situ* and free-ranging populations, regardless of the feeding regimen. In addition, it is recommended that the number and type of measurements obtained, and the methodology used in feeding and observations, be consistent for standardized replication across studies. Wellness checks are generally an ideal time to obtain these physical measurements, but if that is not possible, rough measurements can also be ascertained noninvasively via photographs (Chapter III) taken opportunistically by institutional staff, volunteers, and visitors, or posted on social media (Chapter II). Additional studies are strongly encouraged to continue to improve husbandry practices for *ex-situ* populations, and ultimately, facilitate more effective conservation efforts for free-ranging populations.

References

- Altman, J. D., Gross, K. L., & Lowry, S. R. (2005). Nutritional and behavioral effects of gorge and fast feeding in captive lions. *Journal of Applied Animal Welfare Science*, 8(1), 47–57. https://doi.org/10.1207/s15327604jaws0801_4
- AZA Canid TAG 2012. *Large Canid (Canidae) Care Manual*. Association of Zoos and Aquariums, Silver Spring, MD.
- Bell, K. M., Rutherford, S. M., & Morton, R. H. (2012). Growth rates and energy intake of hand-reared cheetah cubs (*Acinonyx jubatus*) in South Africa. *Journal of Animal Physiology and Animal Nutrition*, 96, 182–190. <https://doi.org/10.1111/j.1439-0396.2011.01133.x>
- Britt, A., Welch, C., Katz, A., Iambana, B., Porton, I., Junge, R., Crawford, G., ... Haring, D. (2004). The re-stocking of captive-bred ruffed lemurs (*Varecia variegata variegata*) into the Betampona Reserve, Madagascar: Methodology and recommendations. *Biodiversity and Conservation*, 13, 635–657. <https://doi.org/10.1023/B:BIOC.00000009497.24917.ae>
- Bryce, C. M., & Williams, T. M. (2017). Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds. *Journal of Experimental Biology*, 220, 312–321. <https://doi.org/10.1242/jeb.144188>
- Cloutier, T. L., & Packard, J. M. (2014). Enrichment options for African painted dogs (*Lycaon pictus*). *Zoo Biology*, 33, 475–480. <https://doi.org/10.1002/zoo.21155>
- Courchamp, F., & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog (*Lycaon pictus*). *Animal Conservation*, 4, 169–174. <https://doi.org/10.1017/S1367943001001196>

- Courchamp, F., Rasmussen, G. S. A., & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13(1), 20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15, 271–274. <https://doi.org/10.1111/j.1523-1739.2001.99534.x>
- Curtis, A. A., Orke, M., Tetradis, S., & van Valkenburgh, B. (2018). Diet-related differences in craniodental morphology between captive-reared and wild coyotes, *Canis latrans* (Carnivora: Canidae). *Biological Journal of the Linnean Society*, 123, 677–693. <https://doi.org/10.1093/biolinnean/blx161>
- Decker, W. (2020). University of Missouri, Missouri Climate Center, College of Agriculture, Food and Natural Resources. Climate of Missouri. <http://climate.missouri.edu/climate.php>.
- Dierenfeld, E. S. (1997). *Captive wild animal nutrition: a historical perspective*. Symposium on ‘Nutrition of wild and captive wild animals’ Proceedings of the Nutrition Society, 56, 989–999. Plenary lecture. Department of Nutrition, Wildlife Conservation Society, Bronx, NY 10460, USA A joint meeting of the Nutrition Society, the Royal Zoological Society of Scotland and the British Federation of Zoos was held at Edinburgh Zoo, Murrayfield, Edinburgh on 16–18 May 1997.
- Hartstone-Rose, A., Selvey, H., Villari, J. R., Atwell, M., & Schmidt, T. (2014). The three-dimensional morphological effects of captivity. *PLoS ONE*, 9(11): e113437 <https://doi.org/10.1371/journal.pone.0113437>

- Hildebrand, M. (1952). *The American Journal of Anatomy. An analysis of body proportions in the Canidae. Volume 90, Number 2*, p. 217–256. Wistar Institute of Anatomy and Biology: Baltimore, MD.
- Hill, R. L., Huskisson, S. M., Weigel, E., & Mendelson III, J. R. (2019). Growth rates of juvenile *Boa constrictor* under two feeding regimes. *Zoo Biology*, 38, 209–213.
<https://doi.org/10.1002/zoo.21460>
- Irwin, M. D., Stoner, J. B., & Cobaugh, A. M. (Eds.). (2013). *Zookeeping: An Introduction to the Science and Technology*. Chicago, IL: University of Chicago Press.
- Kenny, D. E., Mobley, K., Hinkle, S., Bickel, C., Knightly, F., & Laraio, L. (2007). Results of wellness examinations of 28 African hunting dogs (*Lycaon pictus*) puppies at the Denver Zoological Foundation. *Journal of the South African Veterinary Association* (2007) 78(1): 36–39 (En.). Animal Health Department, Denver Zoological Foundation, City Park, E. 2300 Steele St., Denver, Colorado 80205-4899, USA.
- Kilbourne, B. M., & Hoffman, L. C. (2015). Energetic benefits and adaptations in mammalian limbs: Scale effects and selective pressures. *Evolution*, 69, 1546–1559.
<https://doi.org/10.1111/evo.12675>
- O'Regan, H. J., & Kitchener, A. C. (2005). The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*, 35(3&4), 215–230.
<https://doi.org/10.1111/j.1365-2907.2005.00070.x>
- Marsden, C. D., Verberkmoes, H., Thomas, R., Wayne, R. K., & Mable, B. K. (2013). Pedigrees, MHC and microsatellites: An integrated approach for genetic management of captive African wild dogs (*Lycaon pictus*). *Conservation Genetics*, 14, 171–183.
<https://doi.org/10.1007/s10592-012-0440-0>

- Martín-Serra, A., Figueirido, B., & Palmqvist, P. (2016). In the pursuit of the predatory behavior of Borophagines (Mammalia, Carnivora, Canidae): Inferences from forelimb morphology. *Journal of Mammalian Evolution*, 23, 237–249.
<https://doi.org/10.1007/s10914-016-9321-5>
- Meuffels, J., Ververs, C., Pootoolal, J., Langhout, M., & Govaere, J. (2019). Growth, husbandry, and diets of five successfully hand-reared orphaned giraffe calves (*Giraffa Camelopardalis rothschildi* and *Giraffa Camelopardalis reticulata*). *Journal of Zoo and Wildlife Medicine*, 50(1), 205–218.
<https://doi.org/10.1638/2018-0016>
- Rasmussen, G. (1999). Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation*, 99, 133–139.
[https://doi.org/10.1016/S0006-3207\(98\)00006-8](https://doi.org/10.1016/S0006-3207(98)00006-8)
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D.W. (2008). Achilles heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. <https://doi.org/10.1086/590965>
- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286, 232–242.
<https://doi.org/10.1111/j.1469-7998.2011.00874.x>
- Sanz, V., & Grajal, A. (1998). Successful reintroduction of captive-raised Yellow-shouldered Amazon parrots on Margarita Island, Venezuela. *Conservation Biology*, 12(2), 430–441.
<https://doi.org/10.1111/j.1523-1739.1998.96261.x>

- Thomas, P. R., Powell, D. M., Fergason, G., Kramer, B., Nugent, K., Vitale, C., ... Wey, T. (2006). Birth and simultaneous rearing of two litters in a pack of captive African wild dogs (*Lycaon pictus*). *Zoo Biology*, 25, 461–477. <https://doi.org/10.1002/zoo.20111>
- Tutin, C. E. G., Ancrenaz, M., Paredes, J., Vacher-Vallas, M., Vidal, C., Goossens, B., ... Jamart, A. (2001). Framework for the release of wild-born orphaned chimpanzees into the Conkouati Reserve, Congo. *Conservation Biology*, 15(5), 1247–1257. <https://doi.org/10.1111/j.1523-1739.2001.00046>.
- Woodroffe, R., & Sillero-Zubiri, C. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species 2012: e.T12436A16711116. <https://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T12436A16711116.en>. Downloaded on 25 February 2020.
- Wright, W., Smith, H. F., & Grossman, A. (2019). *Hindlimb anatomy of the African painted dog (Lycaon pictus)*. Experimental Biology 2019 Meeting: FASEB Journal. Retrieved from https://www.fasebj.org/doi/10.1096/fasebj.2019.33.1_supplement.615.2

Chapter VI: Conclusion

Anthropogenic activity has been documented to impact the fitness and survival of wildlife (Bessa, Geffroy, & Goncalves-De-Freitas, 2017; Christiansen, Lusseau, Stensland, & Berggren, 2010; French, DeNardo, Greives, Strand, & Demas, 2010; Müllner, Linsenmair, & Wikelski, 2004; Scholten, Moe, & Hegland, 2018; Storch, 2013). Painted dogs are among the species affected by anthropogenic activities, and this dissertation evaluated additional potential direct and indirect anthropogenic threats to them. At first glance, each chapter appears to address distinct or separate topics, yet the chapters are complementary to one another in that they identify ways to move forward with respect to conservation efforts and husbandry practices for captive and wild painted dog populations.

Social media is integral to today's society, and these platforms are used to express a variety of interests through words and images (Fidino et al., 2018). This includes wildlife related posts, which can influence people's actions (Nghiem et al., 2012). YouTube videos, for example, were noted to have positive and negative effects on people's tolerance of wolves (Casola et al., 2020). In Chapter II, using data available via social media platforms, I documented that humans visited painted dog dens in seven of the 14 countries where painted dogs are known to persist: indicating that human disturbance of painted dog dens is occurring in *at least half* of the countries where this endangered species is known to be present. South Africa was a "hotspot" for this activity, but these results may only be the "tip of the iceberg" in identifying the widespread occurrence of this recreational activity. As a popular and profitable activity, it is expected that den visits by humans are occurring in other regions and countries as well. Tourism industry data (e.g., tourist demographics, popular destinations, number of overall visitors to specific African countries) and information relating to access to technology could offer a broader view as to why some countries are over or underrepresented on social media.

Yet it is not enough to simply know where humans are visiting den sites. Assessing factors such as the frequency and time of day of den visits, distance maintained between humans and observed dens, number of humans per visit, method of approach (e.g., by foot or vehicle), and the perception of tolerance of individual and packs of painted dogs are vital. To date, painted dog den visits by humans have not been a cause for alarm in some regions, perhaps due to not being aware of this activity or its potential impacts, or not acknowledging or reporting it. However, future research should be directed at shedding more light on this possibly detrimental tourist activity. It not only directly impacts painted dogs at each den site visited by altering behaviors and activity patterns (Rasmussen & Macdonald, 2012), but may also influence the behavior of other carnivore and herbivore species (Chapter IV), thereby instigating local and landscape level consequences.

Despite the potential negative impacts of den disturbance on painted dogs, social media data such as posts and photos shared by tourists may be useful in monitoring the health and status of painted dogs and other species. Photographs from tourists were used to estimate painted dog numbers in Kruger National Park, South Africa (Maddock & Mills, 1994; Marnewick et al., 2014; Wilkinson, 1995). In addition to helping with population estimates, photos from tourists, recreational ecology studies (Chapter IV), social media, and other sources can be used to identify areas where painted dogs are present, provide an overview of biodiversity, establish a timeline for ecological events, and assess body condition.

Painted dogs were used to develop the noninvasive conservation tool (belly scores) introduced in Chapter III, however, belly scores can be adapted to other species as well. Subjectivity is decreased with the use of the belly score methodology due to the use of specific, identifiable anatomical reference points. The belly score measurement method allowed for a

body condition comparison between two populations of painted dogs in Zimbabwe (Hwange National Park and Mana Pools National Park). This tool provides a quick assessment option for individuals and populations that may offer insight into food stress, foraging success, or seasonal variations (as indicated by the results demonstrating differences between the Hwange and Mana Pools populations), reflecting changes in the populations themselves and the ecosystems they inhabit. Biologically meaningful events were highlighted with the lowest and highest mean belly scores of both populations. The lowest mean belly scores coincided with denning season: an extremely energetically demanding period due to the need to feed adults, quickly growing pups, and resume a nomadic lifestyle as soon as possible. High mean belly scores corresponded to the calving and lambing season of primary painted dog prey species (i.e., kudu [*Tragelaphus strepsiceros*] and impala [*Aepyceros melampus*]): prey is abundant, and adults and pups have access to sufficient food. When used in conjunction with climate and ecological data, belly scores can also provide early indicators of the health of multiple species and ecosystems, and how they may be impacted by climate change.

Belly scores can also be used to compare body condition and fitness among individual painted dogs or packs at zoological facilities. Captive animals are expected to accurately represent their wild counterparts, yet captivity has been demonstrated to alter morphology in various species (Curtis, Orke, Tetradis, & van Valkenburgh, 2018; Dierenfeld, 1997; Hartstone-Rose, Selvery, Villari, Atwell, & Schmidt, 2014; O'Regan & Kitchener, 2005). Collecting and comparing belly scores and other morphometric measurements (Chapter IV) across the life stages of captive animals can offer insight into relationships among genetics, diet, growth, and other factors and assist with improving husbandry practices. Limited staff and funding are common issues for both *in-situ* and *ex-situ* projects. Providing a standardized method for

assessing focal species potentially decreases time and money needed for training and data collection, and allows researchers, institutional personnel (e.g., zoo staff), community members, and tourists to increase or enhance the amount or quality of data collected for analysis.

The results in Chapter IV warrant further investigation. It was proposed that humans unintentionally attract interspecific competitors (i.e., lions and hyenas) to painted dog dens through the action of creating trails when visiting and observing den sites. This scenario was used as a basis to explore the larger issue of carnivore and herbivore use of human-modified game trails (game trails are trails created and used by wildlife) versus unaltered game trails. The expectation was that carnivores would be observed more frequently on trails modified by humans while herbivore presence would be recorded more frequently on unaltered trails. While this trend was observed on average, given the low sample size and loss of data, differences were not significantly different. Data collected via camera traps provided the first general overview of the mammalian community in the study area, however, additional studies are required to further evaluate the overall question of carnivore and herbivore usage of human-modified trails in the study region.

Future recreational ecology studies are encouraged to enhance study design and sampling methods. Suggestions include increasing the sample size (e.g., more cameras, more trails) and sampling across seasons. Creating new trails in any habitat instantly alters the immediate landscape, initiating unknown cascading consequences whether these trails lead to sensitive areas such as painted dog dens or not. Carnivores and herbivores may prefer or avoid human-modified trails, affecting prey availability and predator abundance, thereby increasing energetic costs to painted dogs and decreasing their health, fitness, and survival. The current study focused solely on collecting data during the painted dog's denning season. Yet events outside the denning

season can also influence the presence and behaviors of other carnivores and herbivores, thereby impacting painted dogs and their ecosystems.

The focus shifted from free-ranging painted dog populations in Zimbabwe to a zoological setting in North America in Chapter V where the objective was to explore a possible relationship between feeding regimens and growth in two closely-related painted dog litters. This was done by offering the same diet to both litters via two different feeding regimens (free feed [i.e., access to food throughout the day] and controlled [i.e., access to food twice per day]) and comparing morphometric measurements of pups obtained during 10 and 14-week wellness checks. The two different feeding regimens began when pups were approximately 10 weeks of age. The statistically significant differences in growth over time for each pup was expected. Significant differences in body and hind limb length ratios between litters were not expected, particularly the “kangaroo-like” appearance of Litter B at 10 and 14 weeks. Although the differences in limb length/body length ratios between the litters was not as pronounced at 10 weeks, these results highlight the need for further research relating to diet, feeding regimen, growth, and development in captive and wild painted dog populations, especially if the altered morphology continues into adulthood. Physical changes to a painted dog’s limbs can result in decreased running speeds and stamina, leading to increased energetic costs (which have yet to be explored), decreased foraging success, and increased vulnerability to other carnivores such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*).

The feeding regimen and morphometric measurement comparison between two litters provide baseline data for additional studies relating to the effects of feeding regimens and growth in zoological populations. These types of data are particularly important for individuals targeted for reintroduction or those considered to be genetically valuable. It is recommended that

zoological facilities, conservation centers, and other stakeholders consistently collect data such as belly scores and morphometric measurements for painted dogs and other species of interest across all life stages, some of which can be obtained noninvasively (Chapter II; Chapter III). Standardized collection procedures can help build a substantial dataset that allows husbandry practices to continue to advance for painted dogs and other species.

As conservation is a multi-faceted interdisciplinary endeavor, there is much to consider when moving forward with policies and management plans to address the issues presented here. The following section offers suggestions for future research and management planning.

Future Research & Management Recommendations

The goal of this research was to evaluate potential direct and indirect influences of human activity on free-ranging and captive painted dog fitness and survival during the vulnerable period when they are raising young. Regardless of the threat itself, any anthropogenic impact for any species requires management at multiple levels. As with many human-wildlife interactions, the effects of human activity on painted dogs involves the management of both the species and multiple stakeholders and participants. It is no small feat to get all involved to collaborate, yet that is what must happen to develop sustainable practices and conservation efforts for painted dogs.

The creation and implementation of policies and management programs must occur on a broad scale at all levels (i.e., local, national, international). Of course, policies are not effective unless enforced, and enforcement often requires additional funding and staff. It is beyond the scope of this research to suggest how to best undertake conservation conflict transformation (Center for Conservation Peacebuilding, 2020), however, the nine items that follow are offered for consideration when designing future research and management projects for painted dogs to balance the welfare of this species with human interests.

1. Additional information relating to the scope of painted dog den disturbance is needed.

This may be done via social media, surveys, interviews, datasets from the tourism industry, and/or other methods, but should be inclusive of representatives from multiple areas of interest (i.e., tourists, landowners, local communities, wildlife managers, tourism industry).

2. To coincide with learning more about the location and frequency of den visits, knowing the general den visit guidelines or protocols (if any) that are currently in place is essential. And because the effects of den visits on painted dogs are unknown, it is recommended that a general policy be enacted that requires a specific distance to be maintained between all dens and human visitors. In addition, limits could be placed on the number of visits and/or visitors per den per day, or den sites could be temporarily closed. An assessment of the allowance of on- and off-road access in known denning areas should be conducted; including learning what activities are permitted and what restrictions are imposed during denning season. The following examples provide a starting point. I purposely maintained anonymity here, however, this information is publicly available.

- a. Tour Operator A posted on their blog that a painted dog den site on their property was “open for viewing [because] the pups are old enough to play outside the den, creating a great experience for our guests.” It was also noted that prior to allowing den visits, the den was closed for two months because predators could easily find the den if vehicles drove to the den site too frequently in a straight line.

Precautions taken by this operator were the use of indirect tracks and maintaining

- a 20-meter buffer zone. What was not clearly stated was whether the buffer zone was upheld during both den closure and den visits.
- b. Tour Operator B stated on their website that their den viewing protocol was to allow two vehicles at a time “within the designated area” monitored by camera. There were no further details as to a description of the designated area or how far a vehicle needed to stay from it, however, the operator noted that driving off-road or approaching the area on foot was prohibited.
 - c. Tour Operator C recommended that guests visit during denning season for the best chance to see painted dogs due to the dogs needing to stay in one area. No den viewing protocols were provided on their website.
3. Evaluations of painted dog packs that appear to tolerate human presence near dens would be useful as anecdotal evidence suggests individuals and packs in some regions do not appear to be disturbed by human activity. Questions for assessing similarities and differences between packs that tolerate humans and those that do not include:
- a. What is their reproductive success rate (i.e., litter size, pup survival rate, number of individuals in the pack)?
 - b. Do they den in the same place each year?
 - c. How frequently do they change dens, and do they do so before or after visits by humans?
 - d. What is the distance maintained between the pack, den, and humans?
 - e. Do vehicles stop at the same place for each den visit? Predictability is less threatening to wildlife (Wolf & Croft, 2010), so designating one or two spots at a specified distance from the den may be more acceptable to painted dog packs than

vehicles or humans approaching from multiple directions at different times throughout the day.

- f. Do belly scores and body condition differ significantly?
4. Studies have found that carnivores use human-modified trails for travel, foraging, or territory patrols (Cusack et al., 2015; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Kolowski & Forrester, 2017). This has management implications as altered habitats influence species behavior, affecting other aspects such as predator/prey dynamics and conservation approaches; indicating that human-modified trail usage by carnivores and herbivores may be an issue for painted dogs during their denning season. Further evaluation of this topic in general and how it may affect painted dogs in particular is needed.
5. Consider alternatives and think “outside the box.” Yellowstone National Park prohibits human activity near wolf dens during denning season (Smith et al., 2018) and fencing reduced predation on free-ranging caribou females and calves (Adams et al., 2019). Fencing may not be plausible for painted dogs, but it is important when developing a conservation strategy to research what is being done to protect vulnerable species and populations, as well as being creative about other viable possibilities.
6. Implementation and assessment of the belly score method proposed in Chapter III on other painted dog populations should be employed for health comparisons among and between regional packs and populations.
7. An assessment of educational and awareness programs currently offered in regions where painted dogs are present should be completed. Educational campaigns were helpful in reducing persecution of cheetahs in Namibia (Lindsey, Alexander, du Toit, & Mills,

2005). If not currently in existence, campaigns and programs should be developed and targeted to specific and diverse audiences. For instance, conversations with local ranchers who observe painted dogs on their properties will differ from conversations with tourism industry representatives who are located in a different country; information pamphlets provided to wildlife management agencies would differ from those distributed to tourists and policy makers; and social media posts with conservation messaging may vary depending on the targeted age group.

8. Eliciting collaboration with others who have different perspectives and approaches, even if they appear to be the “opposition,” can be valuable. One example is safari guides who shared when/where they saw painted dogs to assist a group of researchers with their study. Although the primary responsibility of the guides was to locate a trophy species for a client, they were not opposed to assisting with conservation efforts as well.
9. The percentage of people who value watching wildlife over other recreational activities such as hunting and fishing is increasing (Manfredo et al., 2018). With this shift in public values towards wildlife come changes about what is/is not acceptable for managing wildlife, influencing how people will spend their money in relation to wildlife. Data from, and collaboration with, the tourism industry and social scientists can provide insight into how, where, and why people are participating in activities such as den visits, opening up new perspectives and opportunities for understanding, engagement, and compromise.

At the most critical and energetically costly period in a painted dog’s life, human disturbance at painted dog dens can impose additional energetic costs, leading to unknown short and

long-term consequences for this endangered species, their habitat, and the ecosystem. Carnivores are vital to their ecosystems, and particularly vulnerable to effects of human disturbance (Baker & Leberg, 2018). All too often, precautionary measures are either not implemented, or not implemented in a timely manner. In the case of painted dog management plans and policies, it may be prudent to start the conversations about and/or implementation of safety measures such as “buffer zones” for observing painted dog dens in all countries, requiring temporary closure of den sites, limiting the number of vehicles/visitors per den per day, and/or designating one or two specific locations from which to observe dens, sooner rather than later. Compromise is important as the goal is not to eliminate livelihoods or prevent humans from the enjoyment of observing wildlife, but if the safety and welfare of wildlife are not respected, we will no longer have any wildlife to view. This research was conducted with the goal of increasing scientific knowledge of painted dogs and reducing their extinction rate. As cooperative breeders and communal hunters, painted dogs rely on one another (Angulo, Rasmussen, Macdonald, & Courchamp, 2013; Creel & Creel, 2015; Gusset & Macdonald, 2010; Hubel et al., 2016; Rasmussen, Gusset, Courchamp, & Macdonald, 2008; van der Meer, Mpofu, Rasmussen, & Fritz, 2013). We must do the same to change the painted dog’s story from one of persecution and extinction to one of perseverance and survival.

References

- Adams, L. G., Farnell, R., Oakley, M. P., Jung, T. S., Larocque, L. L., Lortie, G. M., ... Russell, D. E. (2019). Evaluation of maternal penning to improve calf survival in the Chisana caribou herd. *Wildlife Monographs*, 204, 5-46. <https://doi.org/10.1002/wmon.1044>
- Angulo, E., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2013). Do social groups prevent Allee effect related extinctions? The case of wild dogs. *Frontiers in Zoology*, 10(11), 1–13. <https://doi.org/10.1186/1742-9994-10-11>
- Baker, A. D., & Leberg, P. L. (2018). Impacts of human recreation on carnivores in protected areas. *PLoS ONE*, 13(4): e0195436. <https://doi.org/10.1371/journal.pone.0195436>
- Bessa, E., Geffroy, B., & Goncalves-De-Freitas, E. (2017). Tourism impact on stream fish measured with an ecological and a behavioural indicator. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 27(6), 1281-1289. <https://doi.org/10.1002/aqc.2804>
- Casola, W. R., Rushing, J., Futch, S., Vayer, V., Lawson, D. F., Cavalieri, M. J., ... & Peterson, M. N. (2020). How do YouTube videos impact tolerance of wolves? *Human Dimensions of Wildlife*. <https://doi.org/10.1080/10871209.2020.1773582>
- Center for Conservation Peacebuilding. (2020). *Center for Conservation Peacebuilding*. Retrieved from <https://cpeace.ngo>
- Christiansen, F., Lusseau, D., Stensland, E., & Berggren, P. (2010). Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endangered Species Research*, 11, 91-99. <https://doi.org/10.3354/esr00265>
- Creel, S., & Creel, N. M. (2015). Opposing effects of group size on reproduction and survival in African wild dogs. *Behavioral Ecology*, 26(5), 1414–1422. <https://doi.org/10.1093/beheco/arv100>

Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T.

(2015). Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE*, 10(5), e0126373.

<https://doi.org/10.1371/journal.pone.0126373>

Curtis, A. A., Orke, M., Tetradis, S., & van Valkenburgh, B. (2018). Diet-related differences in

craniodental morphology between captive-reared and wild coyotes, *Canis latrans*

(Carnivora: Canidae). *Biological Journal of the Linnean Society*, 123, 677–693.

<https://doi.org/10.1371/journal.pone.0126373>

Dierenfeld, E. S. (1997). *Captive wild animal nutrition: a historical perspective*.

Symposium on ‘Nutrition of wild and captive wild animals’ Proceedings of the Nutrition Society, 56, 989–999. Plenary lecture. Department of Nutrition, Wildlife Conservation Society, Bronx, NY 10460, USA A joint meeting of the Nutrition Society, the Royal Zoological Society of Scotland and the British Federation of Zoos was held at Edinburgh Zoo, Murrayfield, Edinburgh on 16–18 May 1997.

Fidino, M., Herr, S. W., & Magle, S. B. (2018). Assessing online opinions of wildlife through social media. *Human Dimensions of Wildlife*, 23(5), 482–490.

<https://doi.org/10.1080/10871209.2018.1468943>

French S. S., DeNardo, D. F., Greives, T. J., Strand, C. R., & Demas, G. E. (2010). Human

disturbance alters endocrine and immune responses in the Galapagos marine iguana

(*Amblyrhynchus cristatus*). *Hormones and Behavior*, 58(5), 792–799.

<https://doi.org/10.1016/j.yhbeh.2010.08.001>

- Gusset, M., & Macdonald, D. W. (2010). Group size effects in cooperatively breeding African wild dogs. *Animal Behaviour*, 79, 425-428.
<https://doi.org/10.1016/j.anbehav.2009.11.021>
- Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. *Biotropica*, 42(1), 126-133. <https://doi.org/10.1111/j.1744-7429.2009.00544.x>
- Hartstone-Rose, A., Selvey, H., Villari, J. R., Atwell, M., & Schmidt, T. (2014). The three-dimensional morphological effects of captivity. *PLoS ONE*, 9(11): e113437
<https://doi.org/10.1371/journal.pone.0113437>
- Hubel, T. Y., Myatt, J. P., Jordan, N. R., Dewhirst, O. P., McNutt, J. W., & Wilson, A. M. (2016). Energy cost and return for hunting in African wild dogs and cheetahs. *Nature Communications*, 7, 11034. <https://doi.org/10.1038/ncomms11034>
- Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE*, 12(10): e0186679.
<https://doi.org/10.1371/journal.pone.0186679>
- Lindsey, P. A., Alexander, R. R., du Toit, J. T., & Mills, M. G. L. (2005). The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biological Conservation*, 123, 229-348.
<https://doi.org/10.1016/j.biocon.2004.12.002>
- Maddock, A. H., & Mills, M. G. L. (1994). Population characteristics of African wild dogs *Lycaon pictus* in the Eastern Transvaal Lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67(1), 57-62.
[https://doi.org/10.1016/0006-3207\(94\)90009-4](https://doi.org/10.1016/0006-3207(94)90009-4)

Manfredo, M. J., Sullivan, L., Don Carlos, A. W., Dietsch, A. M., Teel, T. L., Bright, A. D., &

Bruskotter, J. (2018). American's Wildlife Values: The Social Context of Wildlife Management in the U.S. National report from the research project entitled "America's Wildlife Values." Fort Collins, CO: Colorado State University, Department of Human Dimensions of Natural Resources.

Marnewick, K., Ferreira, S. M., Grange, S., Watermeyer, J., Maputla, N., & Davies-Mostert, H.

T. (2014). Evaluating the status of African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PloS ONE*, 9(1), e86265. <https://doi.org/10.1371/journal.pone.0086265>

Müllner, A., Linsenmair, K. E., & Wikelski, M. (2004). Exposure to ecotourism reduces survival

and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, 118, 549-558. <https://doi.org/10.1016/j.biocon.2003.10.003>

Nghiem, L. T. P., Webb, E. L., & Carrasco, L. R. (2012). Saving Vietnam's wildlife through social media. *Science*, 338(6104), 192–193.

<https://doi.org/10.1126/science.338.6104.192-b>

O'Regan, H. J., & Kitchener, A. C. (2005). The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*, 35(3&4), 215–230.

<https://doi.org/10.1111/j.1365-2907.2005.00070.x>

Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D. W. (2008). Achilles heel of

sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508-518. <https://doi.org/10.1086/590965>

- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286(3), 232–242.
<https://doi.org/10.1111/j.1469-7998.2011.00874.x>
- Scholten, J., Moe, S. R., & Hegland, S. J. (2018). Red deer (*Cervus elaphus*) avoid mountain biking trails. *European Journal of Wildlife Research*, 64(8).
<https://doi.org/10.1007/s10344-018-1169-y>
- Smith, D., Stahler, D., Cassidy, K., Stahler, E., Metz, M., Cassidy, B., ... Koitzsch, K. (2018). Yellowstone National Park Wolf Project Annual Report 2018. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2019-02.
- Storch, I. (2013). Human disturbance of grouse—why and when? *Wildlife Biology*, 19(4).
<https://doi.org/10.2981/13-006>
- van der Meer, E., Mpofu, J., Rasmussen, G. S. A., & Fritz, H. (2013). Characteristics of African wild dog natal dens selected under different interspecific predation pressures. *Mammalian Biology*, 78(5), 336–343. <https://doi.org/10.1016/j.mambio.2013.04.006>
- Wilkinson, I. (1995). *The 1994/1995 wild dog photographic survey*. South African National Parks unpublished report, South African National Parks, Skukuza.
- Wolf, I. D., & Croft, D. B. (2010). Minimizing disturbance to wildlife by tourist approaching on foot or in a car: A study of kangaroos in the Australian rangelands. *Applied Animal Behaviour Science*, 126, 75–84. <https://doi.org/10.1016/j.applanim.2010.06.001>

Appendix A: Permissions

RE: [EXT]: permission to use cheetahandwilddog map?

Fri, Aug 23, 2:01 AM

Dear Tammy,

Thanks for the message and good to hear of your interesting PhD – we will look forward to seeing any publications that come out of that.

Please feel free to use the map and any other data you need off the website. If you need anything else, please just ask. And please credit the Range Wide Conservation Program for Cheetah and African Wild Dogs.

xxx is – as we speak (hopefully!) – busy updating the global wild dog distribution map so it may be that by the time you come to either finishing your PhD and / or publishing that there is a more up to date version. So keep in touch. But for now please go ahead and use the available maps as you need to.

Xxx – any progress with the new map and paper?

Cheers,

xxx

From: Tammy C

Sent: 23 August 2019 01:12

To: xxx

Subject: [EXT]: permission to use cheetahandwilddog map?

Dear xxx and xxx,

I am unsure who to direct my question to, but saw that you are both associated with wild dogs on the Range Wide Conservation Program website. Can you please direct me to the correct contact if neither of you are able to assist me?

I am an American PhD student who is focusing on human-wild dog interactions for my research. My advisor suggested that I include a map of the estimated range of *Lycaon pictus* in my dissertation, and the most current map I've been able to find is on the cheetahandwilddog.org website. I only need to show the "resident" areas, but was told that in addition to citing your website within my dissertation, I need to obtain permission to use your map (even if I'm only using a portion of it). So I am writing to ask permission to adapt your map for my dissertation. I also plan to submit portions of my dissertation for publication in the future and want to be sure that it is okay to use my adaptation of your map there as well (with proper citations of course).

I have attached a copy of the map I plan to use.

Thank you for your time.

Best,

Tammy Cloutier

Environmental Studies PhD Candidate

Antioch University New England

From: Tammy C

Sent: Monday, June 8, 2020 12:11 PM

To: xxx

Subject: Permission request

Good morning xxx,

Do I have your permission to use the illustrations you created (shown below) in my dissertation, dissertation defense presentation, and/or future publications relating to my dissertation? You will be appropriately credited of course.

Tammy

From: xxx

Sent: Monday, June 8, 2020 12:12 PM

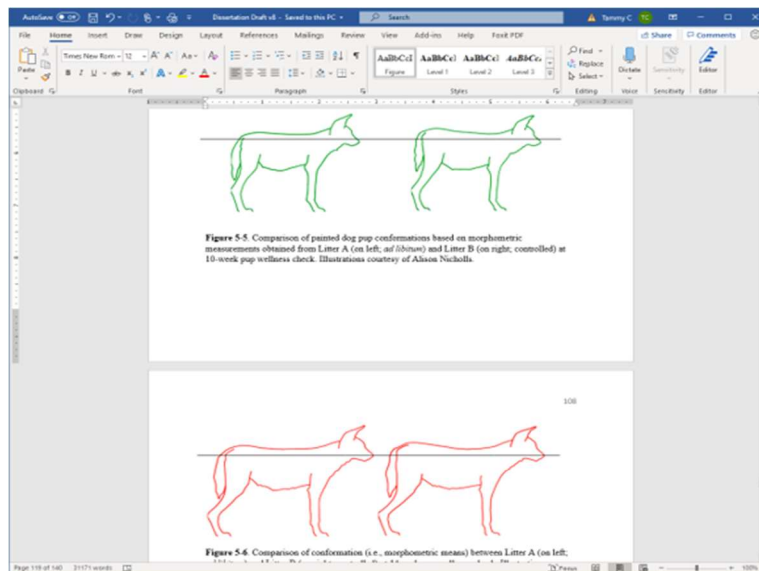
To: Tammy C

Subject: Re: Permission request

Let me think about that....Of Course!!! LOL.

Can't wait to read your dissertation!

xxx



On Mon, Jun 8, 2020 at 8:01 AM Tammy C wrote:

Good morning xxx,

Do I have your permission to use the ESRI GIS map you created for me (shown below) in my dissertation, dissertation defense presentation, an/or any future publications relating to my dissertation? You will be credited appropriately of course.

Tammy

On Mon, Jun 8, 2020 at 12:05 PM xxx wrote:

Hi Tammy,

You may use this at any point in time. Glad it was helpful.

Sincerely,

xxx



Permission request

6 messages

Tammy C

Mon, Jun 8, 2020 at 12:09 PM

To: xxx, xxx

xxx,

Do I have your permission to use the Endangered Wolf Center's painted dog enclosure diagram you created (shown below) in my dissertation, dissertation defense presentation, and/or future publications relating to my dissertation? You will be credited appropriately of course. (PS - had to change the "feet" measurements to "meters" so the numbers are different than what you originally posted.)

xxx,

Do I have your, and hence the Endangered Wolf Center's, permission to use this diagram in my dissertation, dissertation defense presentation, and/or future publications relating to my dissertation?

--

Best,

Tammy

xxx

Mon, Jun 8, 2020 at 4:15 PM

To: Tammy C

Cc: xxx

Yes! You have our permission

xxx

Wed, Jun 10, 2020 at 2:47 PM

To: Tammy C

Cc: xxx

Yes! You have my permission.

Thanks!

xxx

From: Tammy C
Sent: Monday, May 4, 2020 11:21 AM
To: xxx xxx **Subject:** permission to use painted dog pup data?

Hi xxx,

xxx shared a spreadsheet with me when I was collecting data on their painted pup litters in 2019 that lists painted pup weights since 1994. The spreadsheet credits xxx and xxx, and I am writing to ask if that data is published, and if not, do I have permission to incorporate it into one of my dissertation chapters, which will also be submitted to a journal.

My final dissertation chapter focuses on the feeding regimens and morphometric and weight comparisons between the Endangered Wolf Center's 2018 litters. If possible, I would like to compare the weights we obtained with those in your spreadsheet and am happy to answer any questions or offer additional details if needed.

Thank you.

Tammy Cloutier
Environmental Studies PhD Candidate
Antioch University New England

From: xxx
Sent: Monday, May 4, 2020 4:13 PM
To: xxx
Subject: Re: permission to use painted dog pup data?

Those data are not published. You can refer to them as xxx, unpublished data in your dissertation but I would have to be a co-author on any publications resulting from those data.

From: Tammy C
Sent: Monday, May 4, 2020 5:41 PM
To: xxx **Subject:** RE: permission to use painted dog pup data?

That's fair, thank you.

Planning to defend this month or next, so the dissertation chapter will be done soon. I'll let you know when the article is ready to submit for publication.

image permission

3 messages

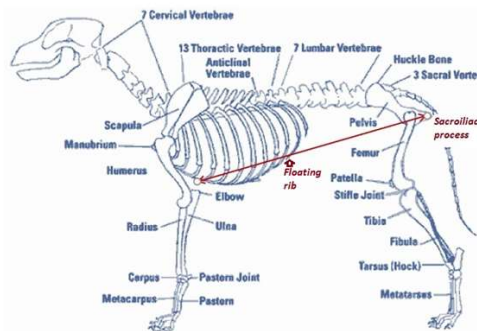
Tammy C

To: xxx

Thu, Aug 13, 2020 at 7:15 AM

Good morning/afternoon,

Do I have your permission to use and alter (e.g., add additional measurements, etc.) your images shown below in my dissertation, dissertation defense presentation, and/or future publications relating to my dissertation? You will be appropriately credited of course.



Tammy

xxx

To: Tammy C

Thu, Aug 13, 2020 at 7:27 AM

Yes, go ahead.